A study of some factors influencing breeding of the kittiwake gull Rissa tridactyla (L.)

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ABSTRACT

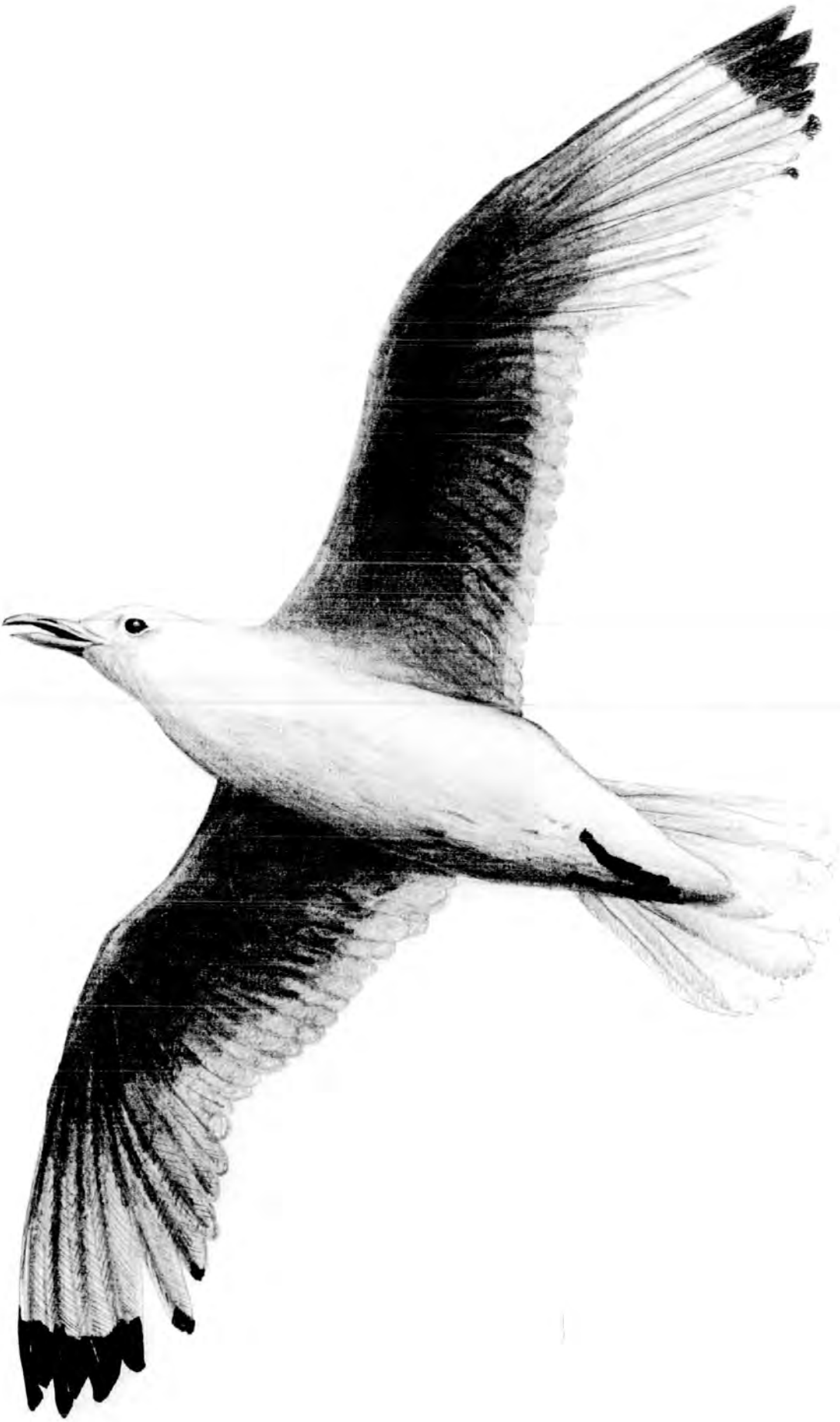
The kittiwake is restricted to breeding within colonies.

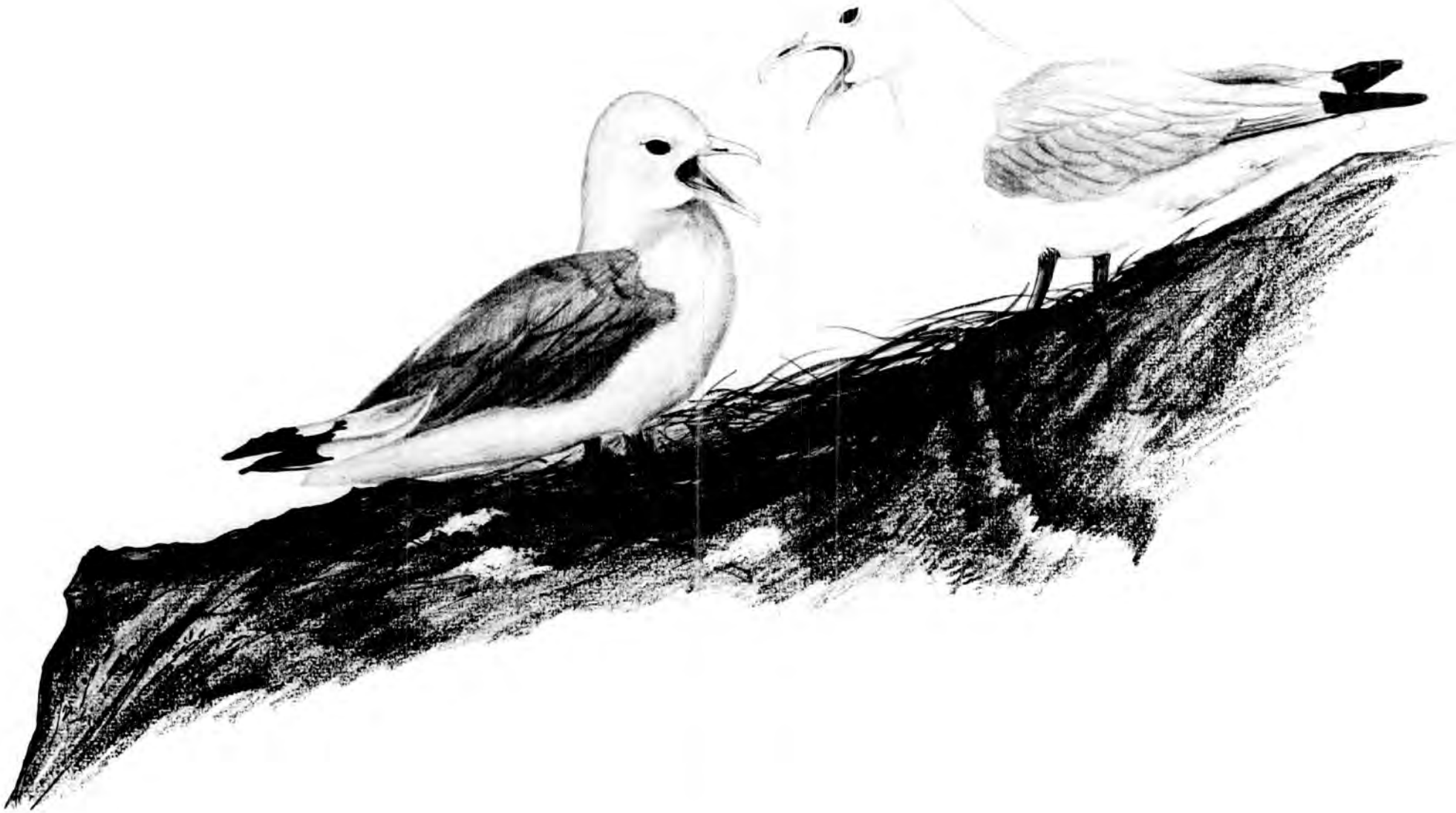
The effect of nesting density on the time of breeding and on breeding success was investigated, at colonies in Northeast England. Evidence exists that the female kittiwake requires stimulation from the mate, and from surrounding pairs, before breeding. The positive effect of nesting density, that is, social stimulation, is mediated through its effect on laying date, resulting in larger clutches of birds breeding at high density. There is a seasonal decline in clutch size. Nesting density has a negative effect on the number of young produced from eggs that hatch, which may be due to the negative action of accepted density dependent factors.

The effect of social stimulation is not restricted to any one year, but is carried forward to the next and subsequent seasons. Birds which breed at high density return to the colony earlier in the following year, and at a more advanced stage of the pre-nuptial moult.

Behavioural studies during the pre-egg laying phase have indicated that the colony, unless very small, never functions as a whole, but as a series of interacting and interlinking groups. The effect of nesting density is not one of mean colony density: the position of the nest within a colony is of importance.

Although it is accepted that there are differences between recruits to high and low density areas, it is proposed that many of the subsequent differences are mediated through the effect of social stimulation on hormone secretion.





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INTRODUCTION

The kittiwake, *Rissa tridactyla*, is a colonial seabird: it is obligatorily colonial, being unable to breed in isolation. Coloniality (breeding groups of aggregated individuals) is a widespread phenomenon in the animal kingdom, occurring in both invertebrates and vertebrates. Among the lower invertebrates the term implies an interdependent physical union; individuals are produced from the same parent stock, and are thus of the same genetic constitution. The members of insect colonies are all closely related; the distinguishing feature of these colonies is the division of labour: individuals are physically separate but dependent on the colony. They show a high degree of altruism, which is better explained by studying the degree of relatedness between individuals (e.g. the close relationship between sisters in Hymenoptera due to the haplo-diploid mode of sex determination (Hamilton 1964)).

Grouping, flocking and colonial breeding in vertebrates have been the subjects of much study, and several advantages in such behaviour have been presented to account for it. Such aggregations, which lack direct physical links, require behavioural adaptations which ensure the cohesion of the group. This may require a complex of special behaviour patterns, as in the truly colonial species, or simpler processes in the less permanent aggregations of animals.

There is considerable evidence to show that groups of individuals are more successful at detecting or deterring predators than isolated pairs or individuals. Most cyprinid fish school in such a way as to confuse predators (Parr 1927); ground squirrels and black-tail prairie dogs have been shown to detect predators earlier when in colonies (Carl 1971, King 1955). Densely nesting guillemots are less vulnerable to predation (Birkhead 1977), and decreased predation is important in maintaining coloniality in sand martins (Hoogland and Sherman 1976).

Another advantage in flocking is in the use of peripheral individuals as a barrier. As predators will tend to take a marginal individual there is an advantage in each individual trying to gain a central position within the group. Movement into the centre of the group is a widespread phenomenon occurring in fish schools, cattle herds, bird flocks and gull colonies. Some bird species flock only when threatened by a predator (Tinbergen 1951, Goss-Custard 1970). In general, fish form more compact schools when fed, but become less aligned when hungry: the advantage in predator avoidance is partially sacrificed for the increased possibility of finding food.

Fraser Darling (1938) first proposed the concept of social stimulation as an advantage in colonial breeding in birds. He suggested that 'The social group and its magnitude in birds which are gregarious at the breeding season are themselves exteroceptive factors in the development and synchronisation of reproductive condition in the members of individual pairs, and throughout the flock.' In effect, there is an enhancement of reproduction by individuals other than the mate; birds nesting at similar densities breed at the same time; those nesting at higher densities breed earlier. It has been shown that for ring doves under experimental conditions the stimulation from the surrounding colony is capable of accelerating reproductive condition over and above that induced by day length and interaction with the mate (Lott, Scholz and Lehrman 1967). Lack and Emlen (1939), in their study of American tri-coloured redwings, found that breeding was more synchronous within three colonies a few miles apart; their breeding periods were not contemporaneous, indicating that the physical states of the birds were influenced by factors other than those of the physical environment. The Darling effect has also been reported in the black-headed weaver (Collias, Victoria and Shallenberger 1971), the gannet (Nelson 1978), Viellot's black weaver (Hall 1970), the

red-winged blackbird (Smith 1943), the equatorial swallow-tailed gull (Hailman 1964) and in the kittiwake (Coulson and White 1960). In all these species synchronisation of breeding activities is greater in local areas. Fisher and Waterson (1941) reported that the social stimulus of numbers in a colony enables fulmars to go through their full breeding cycle. However Lack (1943) noted that this effect may be explained by the differences in the ages of the birds in the different sized colonies.

Several studies have shown that synchrony in breeding may result in more successful breeding due to a swamping effect of the predators (Parsons 1975, Patterson 1965) and/or to benefits derived from social foraging (Emlen and Demong 1975, Horn 1968). Synchronised breeding of unknown origin occurs in social ungulates, and has been reported in the wildebeest (Estes 1966) and African buffalo (Sinclair 1974). The most favoured reason for this is in the swamping of predators: this theory, although attractive, has not yet been adequately tested.

Being the member of a group will reduce an individual's risk of encountering a predator. The advantage of the group increases when the size of the group is above that number taken by a predator on any one encounter.

Ward and Zahavi (1973) presented evidence to support their theory that breeding colonies and other bird assemblages have been evolved primarily for the efficient exploitation of unevenly distributed food sources, acting as information centres. Colonial nesting is primarily adaptive to the variable nature of the food supply in Brewer's blackbird (Horn 1968). The advantage in social foraging is an important factor influencing within-colony breeding synchrony in sand martins (Emlen and Demong 1975). The advantage in grouping for the efficient exploitation of food resources is not restricted to bird assemblages. O'Connell (1960) has shown that, under experimental conditions, schools of Pacific sardines

are more efficient in finding food than isolated individuals. Similarly, some large predatory fish form schools: they themselves have little reason to fear predation.

Wynne-Edwards (1962) has put forward the theory that animal populations can regulate their own numbers in relation to the food available. He has argued that populations rarely increase to such a level that starvation becomes important, and that behavioural mechanisms have evolved which prevent a species outrunning its food supply. Moreover, he suggests that the origin of all social behaviour lies in its function to provide information about population density. At present evidence of this type of system is lacking.

In summary, the four proposed advantages in colonial breeding in birds are social stimulation, population regulation, antipredation and information centres for food finding. The distribution of breeding birds is generally classified as solitary, semi-colonial or colonial; colonial species may also be communal or co-operative breeders. The cause of any one species being colonial may be for one specific reason, or more likely for a complex of more than one of the reasons listed above.

The kittiwake, which nests on cliff ledges, is relatively free from both avian and mammalian predators. It is probably derived from a ground nesting gull, the advantage in cliff nesting being that it reduces predation (Cullen 1957). In contrast to many other avian species, the maximum density of any kittiwake colony is determined by the topography of the rock. All colonies have areas of low density and hence of late breeding. Areas of high nesting density, and hence early breeding, and thus a greater spread of breeding for that colony, are governed by the structure of the cliff. Breeding synchrony is greater in low density colonies, and those with high density have a longer breeding season (Coulson and White 1960).

Kittiwakes, being obligatorily colonial, require more stimulation than can be obtained from their mate. Pairs are unable to breed successfully in isolation. The advantage in social stimulation resulting in more synchronised breeding must be a function rather than a cause of colonial breeding. An assessment of the effects of nesting density on the time of breeding and on breeding success was the main objective of the present study, in an attempt to gain greater insight into the Fraser Darling effect of social stimulation.

BACKGROUND

The breeding biology of the kittiwake has been studied for many years by Coulson at a warehouse colony at North Shields, Tyne and Wear ($55^{\circ}1'N$: $1^{\circ}25'W$). This colony of individually colour-ringed birds, which has been studied since its foundation in 1949, has provided much information on the species. Assumptions made in the present study are upheld by data collected from this colony.

The kittiwake is a long-lived seabird with a low annual mortality: this enables many individuals to breed for several years (Coulson 1966). The age of first breeding is three or four years for the female and four or five years for the male, and breeding success increases with age of the female (Coulson 1966). There is a strong tendency for individuals to retain their mate in successive years: this is more marked in older birds, and in those which bred successfully in the previous year (Coulson 1972). In addition, breeding birds breeding together in successive years tend to hold the same nest site. Thus, courtship continues after pairing, and in each year at the onset of the breeding season.

The study area

The main study area was Marsden Bay, Tyne and Wear (Nat. Grid ref NZ 400 650) where a magnesian limestone stack and mainland cliffs provide nesting ledges for some four thousand breeding pairs of kittiwakes. Figure 1 shows the situation of the colonies. Coulson and White (1956) reported that kittiwakes were first seen in the area in 1930, and that breeding had begun by 1933. Much of the history of the colonies is known (Coulson and White 1958), and the overall growth in breeding pairs is shown in Figure 2. Cormorants and herring gulls nest on the top of the main stack, and fulmars nest on the larger ledges on the stack and cliffs.

Figure 1. The position of colonies at Marsden Bay

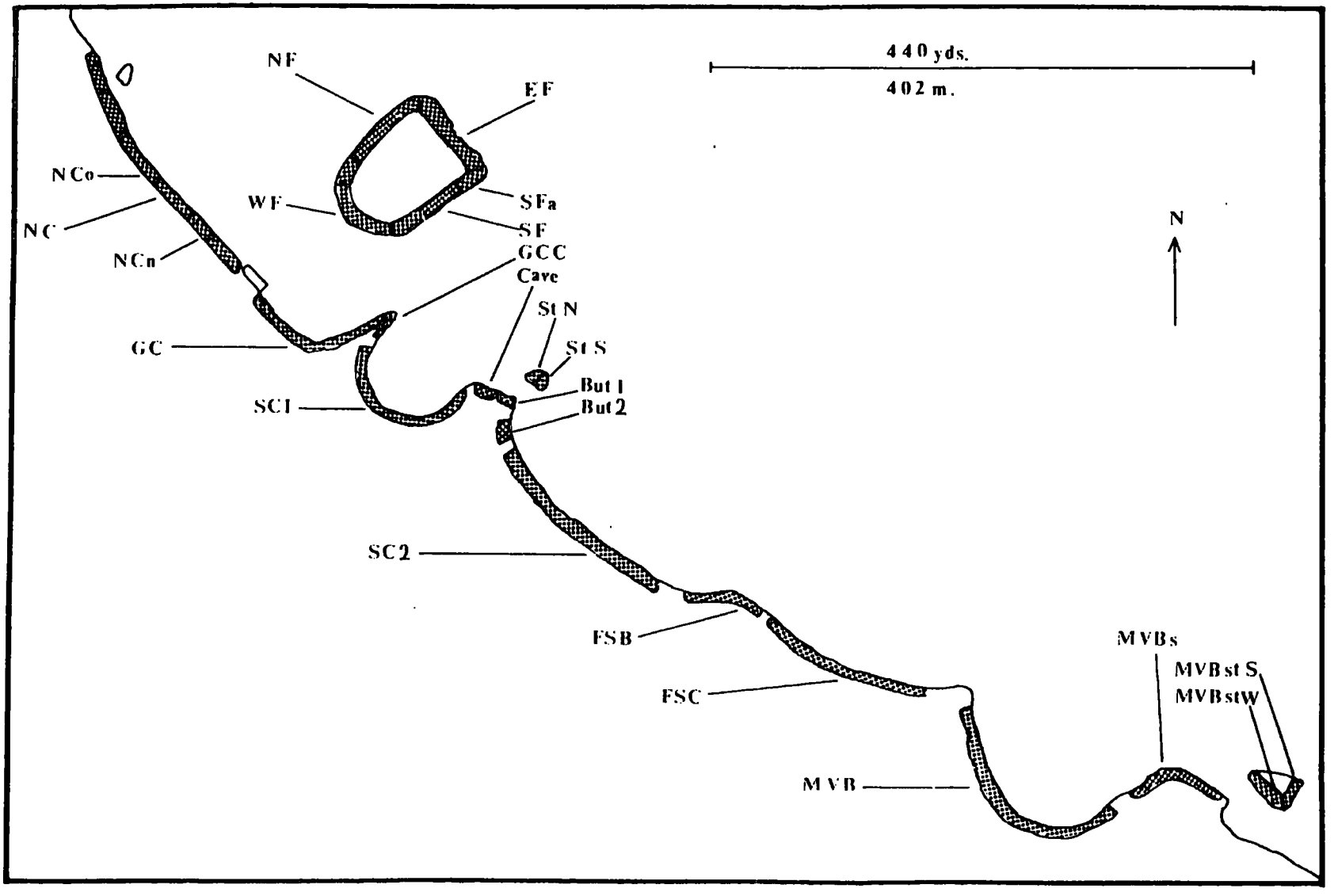
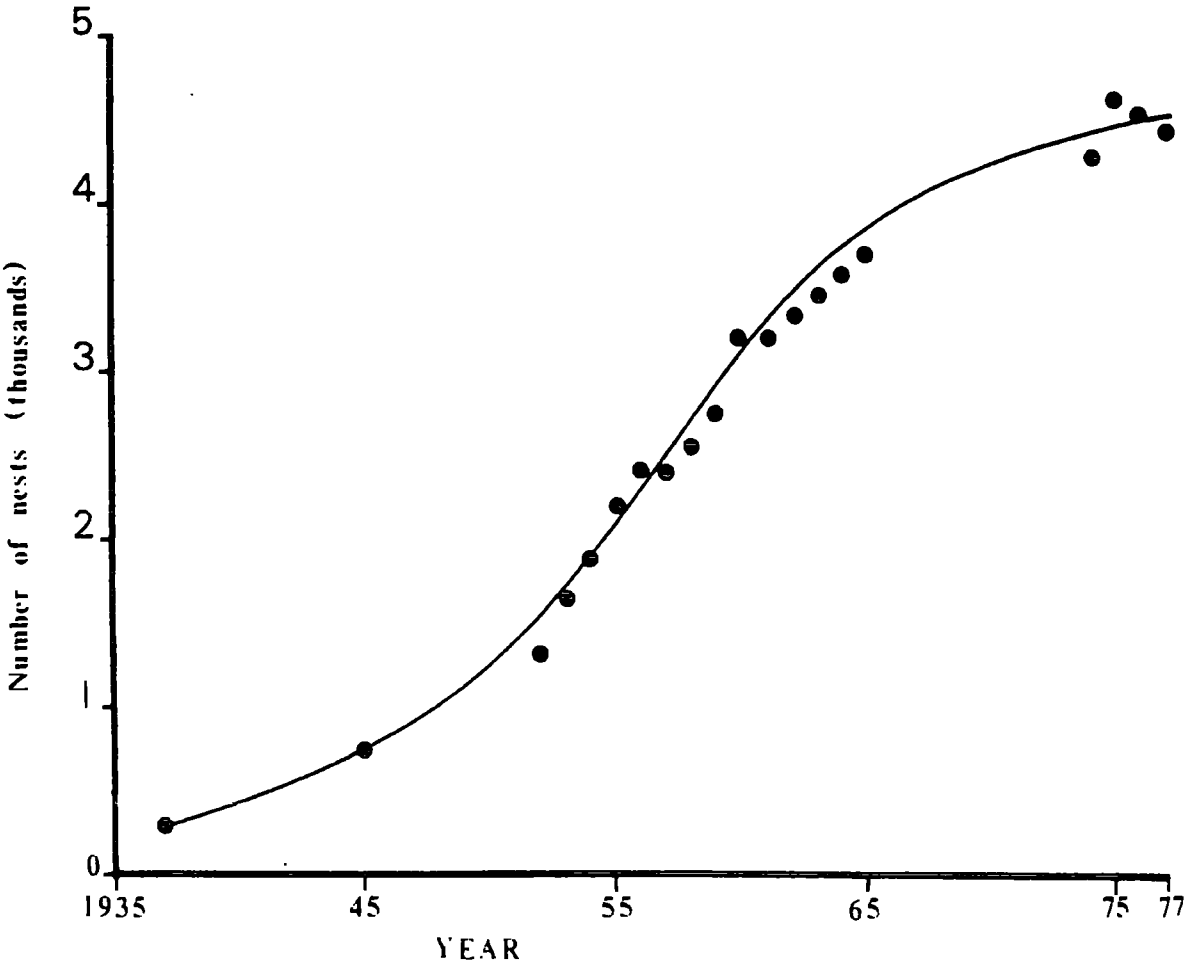
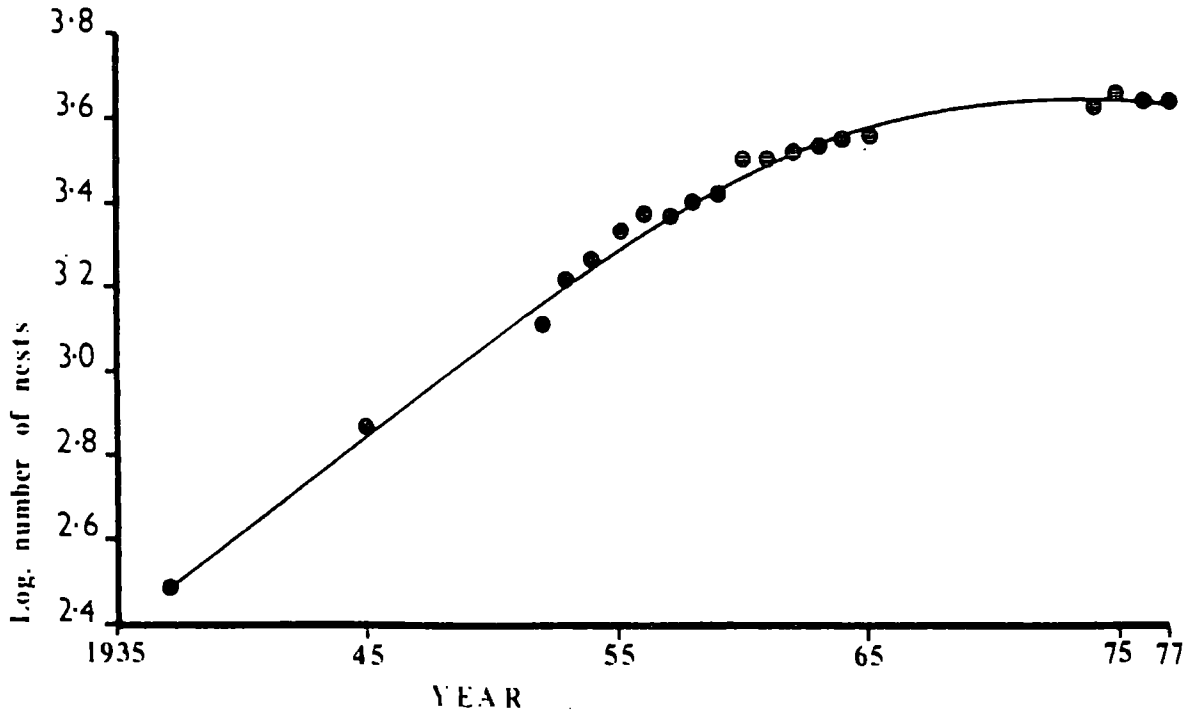


Figure 2. The growth of the kittiwake population at Marsden Bay. The linear relationship of the lower graph between 1937 and 1957 indicates that during this time the population increased at a constant rate. Since then the rate of increase in the number of nest sites has progressively decreased. (The 1937 to 1965 data were supplied by Dr J C Coulson)


5
4
3
2
1
0
Number of nests (thousands)
1935
45
55
65
75
77
YEAR


3·8
3·6
3·4
3 2
3·0
2·8
2·6
2·4
Log. number of nests
1935
45
55
65
75
77
YEAR

The area was divided into twenty colonies according to the topography of the rock. Many of the colonies described by Coulson and White (1956) have increased considerably in size, and in some cases the initial centre of colonisation is no longer the most dense area of the colony. These factors, or changes in rock formation, caused some of the colonies to be given different boundaries.

Although some of the colonies are still increasing, the more dense colonies are decreasing or have reached a saturated level, somewhat below the maximum attained (Table 1). In the densest area, where this was observed, the decrease in nesting density may have been due to the increase in breeding herring gulls immediately above the area, and thus in predation. Similarly, a few sites previously used by kittiwakes were taken over by fulmars.

Five areas were chosen because of their age, density and accessibility at high tide, for detailed study. These were the West Face of the main stack (WF), part of the South Face of the main stack (SFa), two areas of the North Colony (NCn and NCo), and the South Colony One (SC1). The West Face was chosen as there was only one site suitable for mounting a time-lapse camera, and this looked out onto the West Face. Because of the size of the South Face colony (733 nests in 1974), only a portion was studied intensively. The area chosen (SFa, 129 nests in 1974), was the area of greatest nesting density at Marsden and formed the top right hand corner of the South Face. It was therefore bounded on only two sides by breeding kittiwakes. Kittiwakes at Marsden first colonised the main stack: as the colony grew, the mainland cliffs were colonised. The North Colony Original area (NCo) was the initial area of cliff colonisation, and the North Colony New area (NCn) the densest area of the North Colony. The South Colony One area (SC1) was the most accessible low density area. The beach below all low density colonies was cut off at high tide:

the beach leading to the area below the South Colony One was the first to be exposed by the receding tide. These five areas chosen for intensive study are referred to as the main study areas throughout.

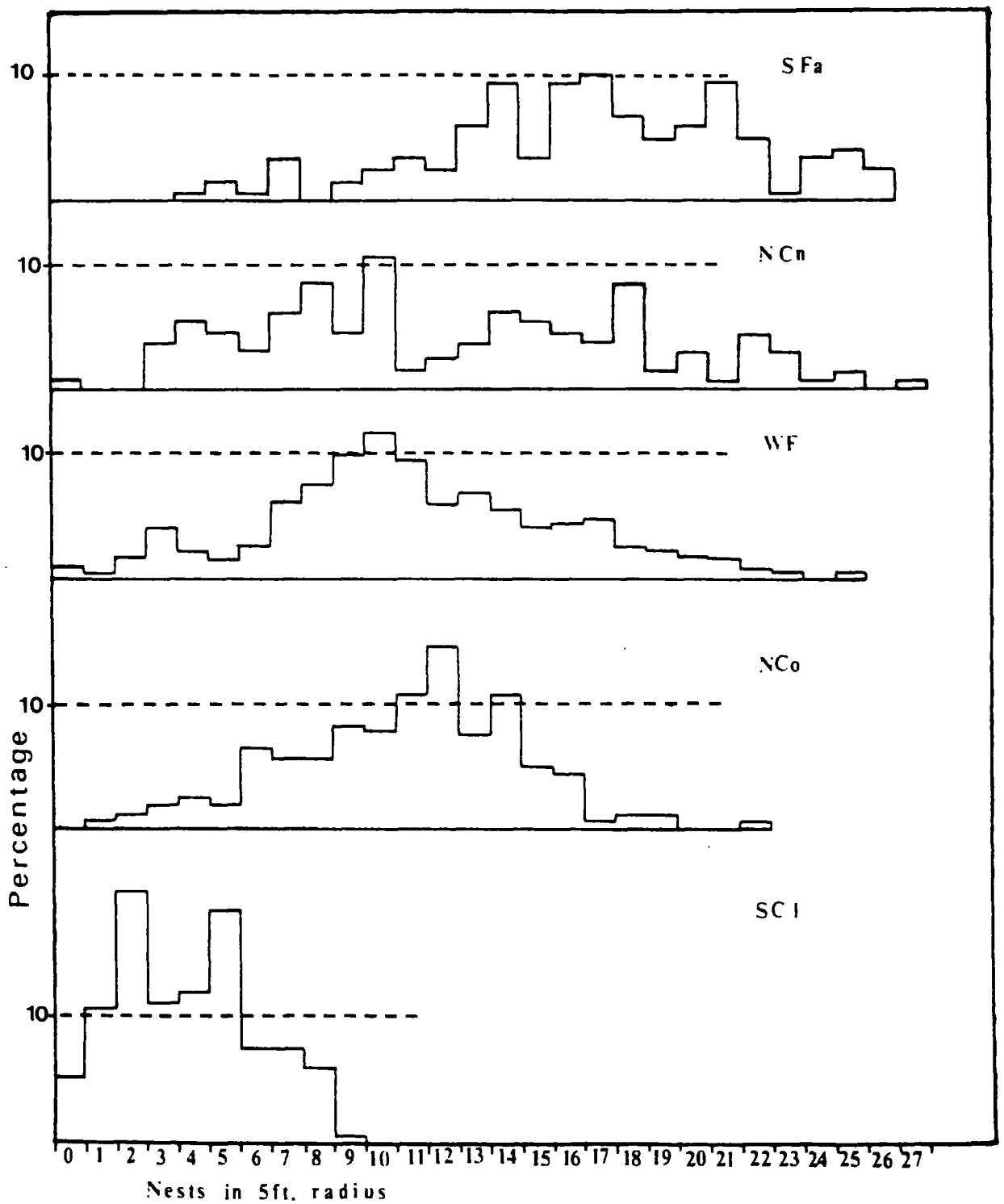
Figure 3 shows the distribution of nest densities in the five main study areas (all colonies have areas of low density, the high density areas have a greater spread of nesting densities). It is notable that the range in nesting density for each colony is greater than that reported by Coulson and White (1960). In their study the maximum number of nests recorded within a five feet radius was twelve: in three of the colonies there are nests with twice this number of nests within a five feet radius. This is discussed further under Nesting Density (see page 13).

Table 1 Nest counts for the 20 Marsden colonies for 1974 to 1977 inclusive

Colony		Year 1974	1975	1976	1977
SF		733	724	711	667
WF		270	267	235	218
NF		436	324	394	383
NC	(1)	120	142	171	193
	(2)	68	74	82	88
NCn	(3)	125	130	118	119
	(4)	152	164	160	176
	(5)	303	313	319	321
	(6)	38	58	57	53
NCo	(7)	157	156	142	126
	(8)	195	186	191	183
	(9)	37	54	43	36
GC		290	310	319	274
GCC		19	31	33	14
SC1		131	150	127	128
CAVE		56	66	68	59
BUT 1		48	51	53	66
BUT 2		158	180	191	202
ST N		9	15	16	17
ST S		27	42	38	35
SC2		165	218	222	218
FSB		80	99	84	97
FSC		185	218	243	217
MVB		128	159	154	172
MVBs		16	28	18	22
MVBst W		56	58	56	61
MVBst S		15	16	16	20
EF		276	301	300	300
(SFa)		129	116	97	115
Total		4293	4534	4561	4465

In 1974, 1975 and 1976 colony nest counts were taken three times between May and June, and the mean number of nests taken as the number of nests in each colony. In 1977 nests were counted once only in late June.

Figure 3 shows the distribution of nest densities in the five main study areas in 1975. The number of other nests within a five feet radius of each nest was recorded and the number in each density group expressed as a percentage of the total number of nests in the colony. The dotted line indicates the 10% level. It is notable that the range in density is greater in the high density colonies, and that the range in nesting density for each colony is greater than that reported by Coulson and White (1960). (In their study the maximum number of nests recorded within a five feet radius was twelve.)

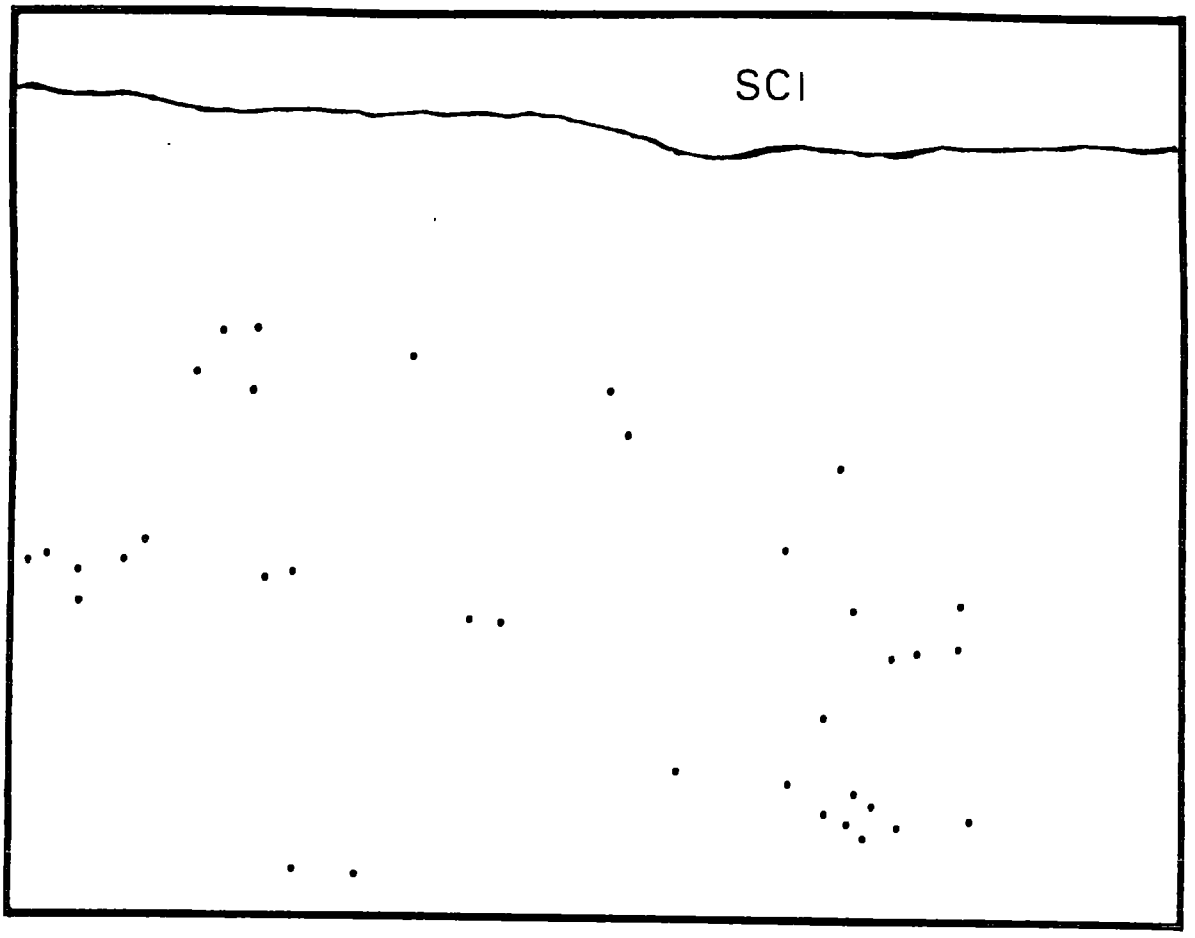

SFa
NCn
WF
NCo
SCI
10
Percentage
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27
Nests in 5ft. radius

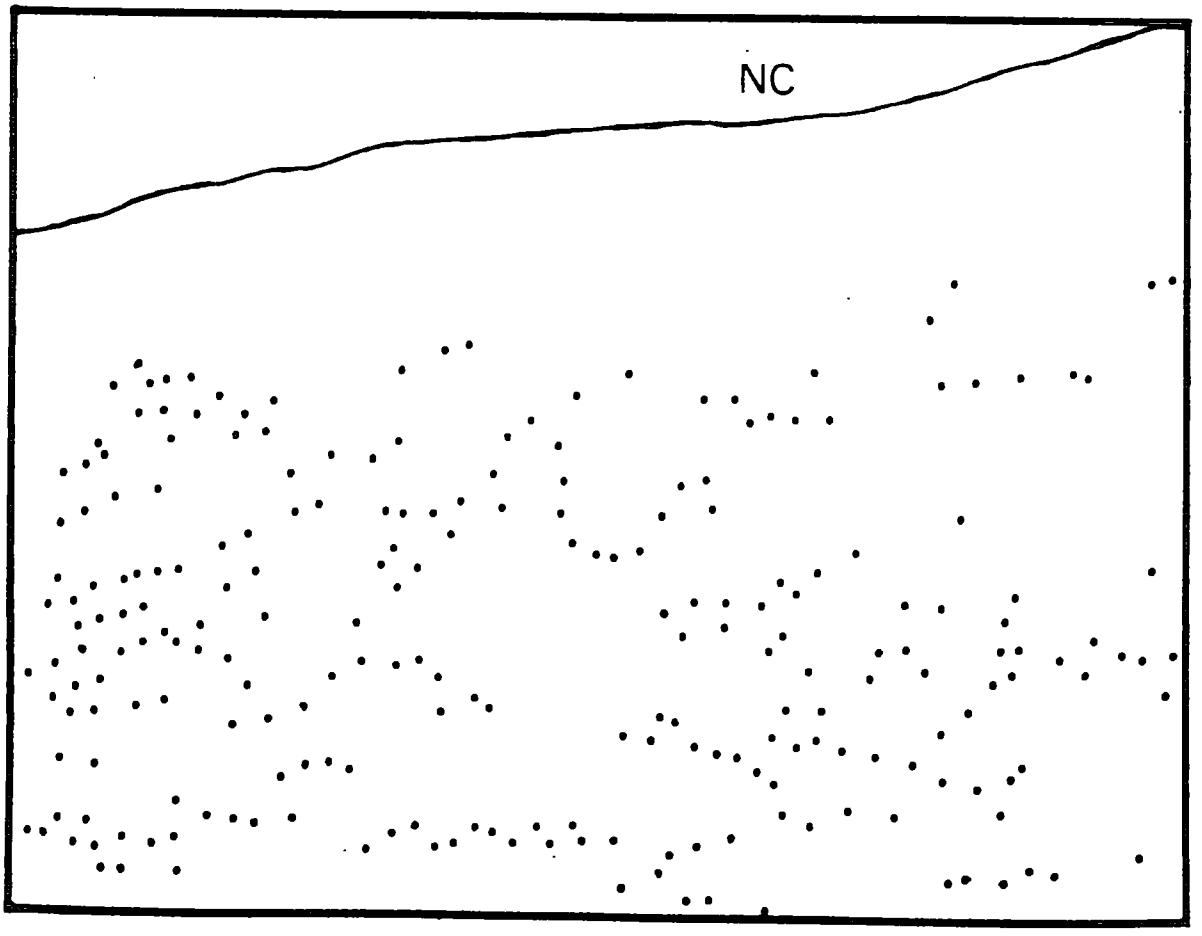
NESTING DENSITY

The basis of this research was to study the effect of nesting density on breeding success and on the time of breeding. As such, the method used in measuring nesting density is of considerable importance. Various methods are possible, but each has its own limitations. Although kittiwakes aggregate for breeding, they are not evenly distributed within an area. In general, nests in high density areas have consistently high values for the number of nests at successive distances from them, and low density areas have consistently low values. Figure 4 shows the position of nests in parts of two of the main study areas (North Colony New area, NCn, and South Colony One, SCl). Clumping of the nests is more evident in the low density colony and here the described relationship does not hold. Because of local clumping, such methods as nearest neighbour and closest individual techniques, giving a mean value of nests per unit area, will tend to give exaggerated density values for low density colonies. Further, the biological significance of nesting density must be considered. A mean value of nests per unit area for each colony takes no account of the distribution of nests within that unit area, although such values will serve to compare high and low density colonies. It must be considered, and could be expected, that nests in close proximity with another will have a greater effect than those further away. For these reasons the methods used in measuring nesting density were as follows.

The main study areas were photographed and each nest numbered on an enlarged print. The normal kittiwake nest is 12 inches (one foot) in diameter, and because of this all density measurements were calculated in feet. The diameters of twenty nests were measured on each photograph, and the mean value of nest diameter taken as a standard of one foot (0.305m). With the use of a perspex overlay on which concentric circles were etched

Figure 4. The position of nests in areas of two of the colonies (North Colony, NC, and South Colony One, SC1), showing local clumping of nests. Clumping is more evident in the low density colony (SC1) and is due in part to the structure of the rock


SCI


NC

at the equivalent of 1, 2, 3, 4, 5 and 10 feet from the centre, the number of nests within each area was recorded for each nest (i.e. within the areas of 0-1, 1-2, 2-3, 3-4, 4-5, 5-10 feet of each nest).

Additionally for the main study areas, and for all other colonies, a density measure was obtained by the boundary strip method (Southwood 1966). On an enlarged photograph of each colony a line was drawn joining the peripheral nests, and a line drawn at the equivalent of five feet outside the former boundary. The area of the colony was calculated from this, and the mean number of nests within 78.5 square feet (the area of a circle with a radius of five feet) was calculated (78.5 sq ft = 7.3 sq m).

Behavioural studies of the infectious nature of the greeting ceremony, during the pre-egg laying period, have indicated that pairs responded to others over a distance of approximately five feet (Chapter 6, page 52). As it is likely that this behavioural response is an important source of stimulation for the kittiwake, the mean number of other nests within a radius of five feet was used as a measure of effective nesting density.

Because of the method used in taking the standard of one foot, from the diameter of twenty nests, an element of subjectivity is introduced. Although consistent within this study, the actual boundary (diameter) of the nest may have been greater than that used by Coulson and White (1960). The area used for kittiwake nest sites on the main stack has remained more consistent than the areas of mainland cliff colonies, the latter having increased in size considerably since the study by Coulson and White. In an attempt to assess how much the method employed caused the differences in density reported here and those reported by Coulson and White (1960), the nesting density of the South Face colony was calculated for 1958 from photographs. The South Face colony as described by Coulson and White (1960)

incorporated the West Face colony which in 1958 was a small low density peripheral area of the South Face. (The South Face and West Face together will be described as the South Face C Colony.)

Initially a colony density measure for the South Face C Colony in 1958 was calculated, by again taking a standard of one foot, and by using the boundary strip method. The mean nesting density of the South Face C Colony was calculated to be 11.33 nests/78.5 sq ft (cf. 7.95 reported as the nesting density of the South Face C Colony in 1958 by Coulson and White (1960)). Their method involved calculating the area of a rectangle of cliff, which was drawn ten feet outside one bounding peripheral nests. The area of cliff used was thus greater than that used in the present calculation for 1958. Nonetheless, calculations using the boundary strip method show that the nesting density of the South Face Colony increased by 5.3% between 1958 and 1975, and the nesting density of the West Face by 225% over the same period.

Both increase in nesting density and the method employed have given rise to the fact that the present density measures are higher than those reported by Coulson and White (1960).

Low density colonies at Marsden could be expected to have increased in density more than the high density South Face colony, in that the overall number of nests at Marsden increased by 74% between 1958 and 1975.

To assess the consistency of the one foot standard, the number of nests with no others within a radius of five feet, and the number of nests with one other within a radius of five feet, were calculated. A small discrepancy in the measure will obviously be of significance when determining the actual number of nests within a five feet radius. If, for example, a standard of not one foot but 1.1 feet is compared with a standard of one foot, the result is in an increase of 21% in the area of a 'five feet' radius circle. Coulson and White (1960) reported 1.5% of

nests in the South Face C colony with no other nests within a radius of five feet, and 4.5% of nests with only one other within a five feet radius; by using the same method, I obtained 1.0% of the nests with no others within a radius of five feet, and 1.4% of nests with only one other within a radius of five feet. The standard of 'one foot' used in the present study is therefore greater than that used by Coulson and White. This discrepancy in the measure must be considered when any literal comparison between nesting density in the two studies is made, although the evidence shows that both the method employed, and the fact that nesting density has increased, have given rise to the differences in the values of nesting density reported by Coulson and White, and those in the present study.

Clumping occurs in only a small proportion of nests: because of this there are positive correlations between successive density values obtained for each nest in the main study areas (Table 2 for 1975; Table 3 for 1976). It is notable that all correlations are positive, and that values increase down the table.

As the area of concentric circles increases as the distance from the centre (nest) increases, the number of nests increases. For example, there are more nests two to three feet from a nest than one to two feet from it, and this is shown in Table 4 which gives the mean nesting densities at successive distances from each nest. Because of this, there is potentially greater variation in the number of nests at increasing distances, and thus greater possibility of increased correlations between the higher density values of areas further from a nest. In addition, the percentage of nests with no nests within each area decreases as the area increases (Table 5). The successive increase in correlation coefficients at increasing distances from the nest are due to this, as are the increases in regression coefficients across the Tables 2 and 3.

Tables 2 and 3 show the correlation coefficients and regression coefficients between density values for 1975 and 1976.

As the area of concentric circles increases with distance from the centre (nest), the number of nests within each area increases. There is, therefore, potentially greater variation in the number of nests at increasing distances, and the increased possibility of increased correlations between higher density values of areas further from the nest. In addition, the number of nests with no nests within each area decreases as the area increases. The successive increase in correlation coefficients at increasing distances from the nest, and the increases in regression coefficients across the tables, are due to this.

Table 2. A) shows the correlation coefficients (all positive) between density values of all nests in the main study areas in 1975, together with the mean number of nests in each area, and the standard deviation, based on 814 nests.

B) shows the regression coefficients (all positive) between density values in 1975, based on 814 nests.

A) Density	1-2'	2-3'	3-4'	4-5'	5-10'	$\bar{x}$ ± S.D.
0-1'	0.200	0.190	0.211	0.175	0.233	0.447* 0.704
1-2'		0.407	0.330	0.287	0.378	1.909 1.558
2-3'			0.417	0.373	0.457	2.373 1.785
3-4'				0.479	0.528	2.725 2.059
4-5'					0.519	3.274 2.286
5-10'						22.287 11.748

B) Density	1-2'	2-3'	3-4'	4-5'	5-10'
0-1'	0.442	0.482	0.615	0.569	3.722
1-2'		0.466	0.435	0.421	2.853
2-3'			0.481	0.477	3.004
3-4'				0.532	3.011
4-5'					2.667

0-1' = the number of nests within one foot of a nest

1-2' = the number of nests between one and two feet from a nest etc.

$\bar{x}$ ± S.D. = the mean number of nests within each area and its standard deviation

* = the mean nest density of the 0-1' area is a measure of the mean number of other nests within that area, for each nest. The true value should thus be increased by one, to include the central nest from which measurements were taken.

Table 3. A) shows the correlation coefficients (all positive) between density values of nests in the main study area in 1976, together with the mean number of nests in each area and the standard deviation, based on 614 nests

B) shows the regression coefficients (all positive) between density values in 1976, based on 614 nests

A) Density	1-2'	2-3'	3-4'	4-5'	5-10'	$\bar{x}$	± S.D.
0-1'	0.216	0.204	0.174	0.185	0.228	0.443*	0.682
1-2'		0.411	0.318	0.284	0.378	1.888	1.537
2-3'			0.434	0.355	0.493	2.334	1.740
3-4'				0.465	0.546	2.648	1.972
4-5'					0.539	3.252	2.260
5-10'						21.695	11.554

B) Density	1-2'	2-3'	3-4'	4-5'	5-10'
0-1'	0.486	0.520	0.503	0.615	3.872
1-2'		0.465	0.408	0.418	2.841
2-3'			0.491	0.461	3.276
3-4'				0.533	3.199
4-5'					2.757

0-1' = the number of nests within one foot of a nest

1-2' = the number of nests between one and two feet from a nest etc.

$\bar{x}$ ± S.D. = the mean number of nests within each area and its standard deviation

* = the mean nest density of the 0-1' area is a measure of the mean number of other nests within that area, for each nest. The true value should thus be increased by one, to include the central nest from which measurements were taken.

Table 4. The mean nesting density values for the five main study areas in 1975, together with the standard deviation and sample size. As the area of concentric circles increases with the distance from the centre (nest) the number of nests within each area increases

Colony	Number of nests											
	0-1'		1-2'		2-3'		3-4'		4-5'		0-5'	N
	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	
WF	0.56	0.74	1.96	1.43	2.72	1.78	2.66	1.81	3.26	2.13	11.16	267
NCn	0.59	0.72	1.97	1.44	2.36	1.70	3.14	2.15	4.24	2.52	12.30	130
NCo	0.30	0.57	1.80	1.26	2.28	1.39	2.76	1.50	3.61	1.86	10.75	156
SCl	0.08	0.28	0.81	0.85	0.82	0.94	0.90	0.97	1.14	1.00	3.75	145
SFa	0.68	0.90	3.26	1.93	3.67	1.78	4.64	2.21	4.44	2.25	16.69	116
Total mean	0.45	0.70	1.91	1.56	2.37	1.79	2.72	2.06	3.27	2.29	10.73	814

0-1' = the number of nests within one foot of a nest

1-2' = the number of nests between one and two feet from a nest etc.

Table 5. The percentages of nests in each colony which have no other nests within the areas of 0-1, 1-2, 2-3, 3-4, 4-5 and 5-10 feet from them. As the area of concentric circles increases with distance from the centre (nest) the number of nests within each area increases. Associated with this, the percentages of nests with no other nests within each area decrease as the area increases. The low density areas have more nests with no other nests within each area.

1975

	Distance from the nest					
Colony	0-1'	1-2'	2-3'	3-4'	4-5'	N
SFa	56	8	1	1	2	116
WF	57	15	7	9	7	267
NCn	54	11	11	5	4	130
NCo	76	15	9	3	3	156
SCl	92	42	47	40	27	145
Mean	66	18	14	12	9	814

In both the analyses of factors affecting hatching date and of those affecting the number of chicks fledged, multivariate stepwise regression analyses have been used with density values as independent variables. Although they remain true independent variables, because of the correlations between them, the results obtained were in some cases misleading, and care has been taken to avoid erroneous conclusions being drawn. For example, in the multivariate stepwise regression analysis of factors affecting hatching date in 1976, both one to two feet density and five to ten feet density were significant factors, but within one foot density, two to three feet density, three to four, and four to five feet densities were omitted. Although the analysis is statistically correct, it makes little sense biologically to have chosen the one to two feet density value in preference to the within one foot density value.

When any one density value is introduced as an independent variable into the equation of a multivariate stepwise regression analysis, the correlation of other density values with the residual variance is reduced. If a second density value subsequently enters the equation, it may be that it describes a negative relationship when the initial density described a positive relationship. The initial chosen value having a positive relationship will have removed much of the effect of the following density value, and the latter, when later introduced, may describe the spread of the relationship and thus exhibit negative correlation and regression coefficients. Moreover, the choice of different density values in equivalent analyses in successive years may not indicate real differences in the two situations; for example, by chance variation three feet density may fit the data of hatching date better than four feet density which was chosen in the previous year. This effect is again due to the correlations between successive density values, and higher correlations associated with an increase of nests in the larger areas.

OCCUPATION OF THE COLONIES

Previous studies of kittiwake breeding biology have indicated that nesting density is an important factor in determining the time of breeding (Coulson and White 1960). As nesting density can only have a stimulatory effect when the birds are present at the colony, the annual reoccupation and vacation of the colonies were investigated.

Methods

The number of sites occupied and the number of pairs present at all colonies were counted at least once each week between 10.00 and 13.00 G.M.T. during 1974 and 1975 throughout the period of occupation, and in 1976 during the period of reoccupation. The nests in the five main study areas were each numbered on an enlarged photograph of each area. These areas were photographed weekly to give data on the occupation of the individual sites. The West Face was also studied with the use of time-lapse photography. Photographs were taken every ten minutes from dawn to dusk twice weekly throughout the 1974 breeding season, and much of the 1975 season. Several days' data were lost in 1975 due to a failure of the automatic light meter on the camera. On each visit to the colony the camera was set to film on the following day. During the early part of the season some of the films were of poor quality due to heavy sea-mist, rain and occasionally other adverse weather conditions. Standard 35mm, black and white, 400 ASA film was used, and the projected negatives provided enough detail for direct analysis.

Panic flights

Panic flights were first described by Kirkman (1937) as upflights of the black-headed gull: they also occur in common and arctic terns, and are used to deter avian predators. In the kittiwake, during the early part

of the season, these flights appear spontaneously without an obvious stimulus, or in response to the appearance of a low flying aircraft or helicopter, which presumably simulate an avian predator. The birds leave the nest site with a characteristic dive, and then fly rapidly out to sea: the whole activity takes place in complete silence, in contrast to the normal conditions at a colony.

The return

Many seabird species spend longer at their nest site than required for nest building and breeding (Coulson and White 1958, Belopol'skii 1961, Birkhead 1977), and this is true of the kittiwake. The reoccupation of the colonies is a gradual process which takes place over several weeks. Coulson and White (1956) have described this for the colonies at Marsden, and although the general pattern of behaviour remained the same, the time and order of return differed from their findings. The first stage of the reoccupation is not the presence of birds on their nest sites, but the presence of a raft of birds some 100-200 yards offshore. These rafts form early in the morning and are present until about noon, when the birds fly out to sea together. The rafts were not formed in windy weather. The size of the rafts increases daily until as many as three hundred birds may be present (Table 6). From the time that the rafts contain about thirty individuals, birds leave the raft in a synchronised group and fly in towards the cliffs, fly past, and then out to rejoin the raft. This is repeated until eventually some of the birds land on the sites, where they remain for a few minutes only. When on the sites the birds are extremely alert and uneasy: they soon leave the colony in a panic flight and return to the raft. By the time that 60% of the sites are regularly occupied, the rafts are no longer formed: the birds fly straight in from the sea in the early morning.

Table 6 The size of rafts seen off the South Face Colony in 1975, and the number and percentage of nest sites occupied on the South Face. The rafts form early in the morning and are present until noon when the birds fly out to sea together. Rafts are not formed in windy weather. (It is notable that on 23.1.75, when no raft was formed, the mean daily wind speed was 16.7 knots.) The size of the rafts increases daily: by the time that 60% of the sites are regularly occupied, the rafts are no longer formed.

Date	Raft size	Number of sites occupied	Percentage of sites occupied	Mean daily wind speed (knots)
6.1.75	0	0	0	23.1
7.1.75	30	129	17	10.4
9.1.75	70 - 100	113	16	12.4
14.1.75	200	32	4	14.5
17.1.75	300	313	43	5.7
23.1.75	0	212	29	16.7
27.1.75	80 - 100	425	59	9.1

Never was a single bird seen to fly in from a raft and occupy an empty colony. At least ten, and usually about forty birds would fly in together, and some occupy sites. The departure from the colony was less synchronised, with single birds occasionally being seen on large areas of cliff, but for short periods only. Birds appear to require the stimulation from other birds to overcome the urge to stay at sea, and to satisfy the breeding drive to come ashore and occupy the nesting ledges. No correlation was found between the numbers of birds initially colonising an area and either the density of birds, or the nest density of the colony. As the birds involved in the initial reoccupation are the older birds, and those returning to their sites of the previous year, such a relationship would be unexpected. A clear threshold level of the number of birds reoccupying a colony was not evident, although it can be said that single birds were never seen to occupy empty colonies.

The return and build-up of numbers of birds in the main colonies are shown in Figure 5, for 1975, by expressing the number of sites occupied as a percentage of the subsequent nests in that colony. The return is gradual, starting in early January each year, and the order of return was much the same in the three years studied. This order is not that of initial colonisation, but closely follows the order of mean nesting density (Table 7). The differences between the colonies are smaller than those reported by Coulson and White (1956) who found that the order of return was the same as that of colonisation in both 1953 and 1954. During this period, the lower density colonies were rapidly increasing in size and therefore had a higher percentage of young birds, returning later, which could have given rise to the greater variation between colonies.

The effect of colony mean density on the date of return to the five main study areas was investigated. Figure 6, the percentage of sites occupied against density for eleven dates during January and February and

Figure 5 The return and build-up in numbers of birds in the main colonies in 1975. The number of sites occupied is expressed as a percentage of the subsequent nests in that colony and plotted against date. The reoccupation of the colonies is a gradual process which takes place over several weeks: there are differences in the dates of return to the different colonies.

A shows the return to the South Face colony (SF) and Marsden Village Bay (MVB)

B shows the return to the South Face colony, the West Face colony (WF), and the Far South Colony (FSC)

C shows the return to the South Face colony, the North Colony (NC), and the South Colony Two (SC2)

D shows the return to the South Face colony, the Grotto Colony (GC), and the South Colony One (SC1)

E shows the generalised pattern of return to two hypothetical colonies.

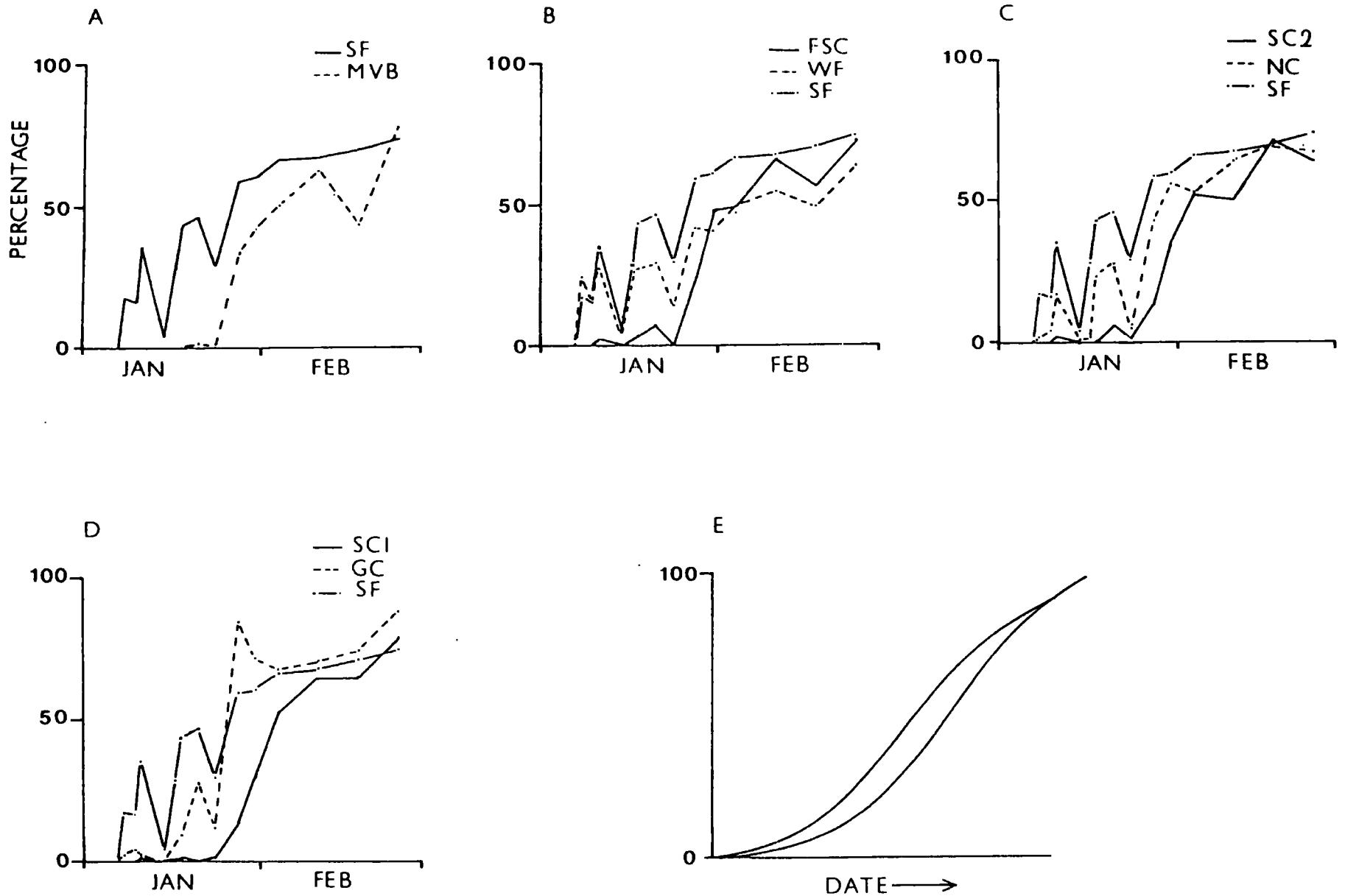

A
SF
MVB
100
50
0
PERCENTAGE
JAN
FEB
B
FSC
WF
SF
100
50
0
JAN
FEB
C
SC2
NC
SF
100
50
0
JAN
FEB
D
SCI
GC
SF
100
50
0
JAN
FEB
E
100
0
DATE

Table 7 The order of return to the colonies in 1974, 1975 and 1976 follows that of mean nesting density and not that of initial colonisation. The differences between the colonies are less marked than those found by Coulson and White (1956) when the low density colonies were rapidly increasing. The magnitude of the differences are shown for 1975 in Figure 5, and tabulated below.

Colony	Breeding first reported	Order of colonisation	Order of return 74	75	76	0-5' density
SF	1933-37	1	1	1	1	16.4
WF	1933-37	2	2	2	2	13.2
NC	1941-45	4	3	3	3	9.3
GC	1950	6	4	4	4	4.3
SC2	1940	3	6	6	6	2.2
FSC	1947	5	5	5	7	3.1
MVB	1953	7	?	7	5	3.4

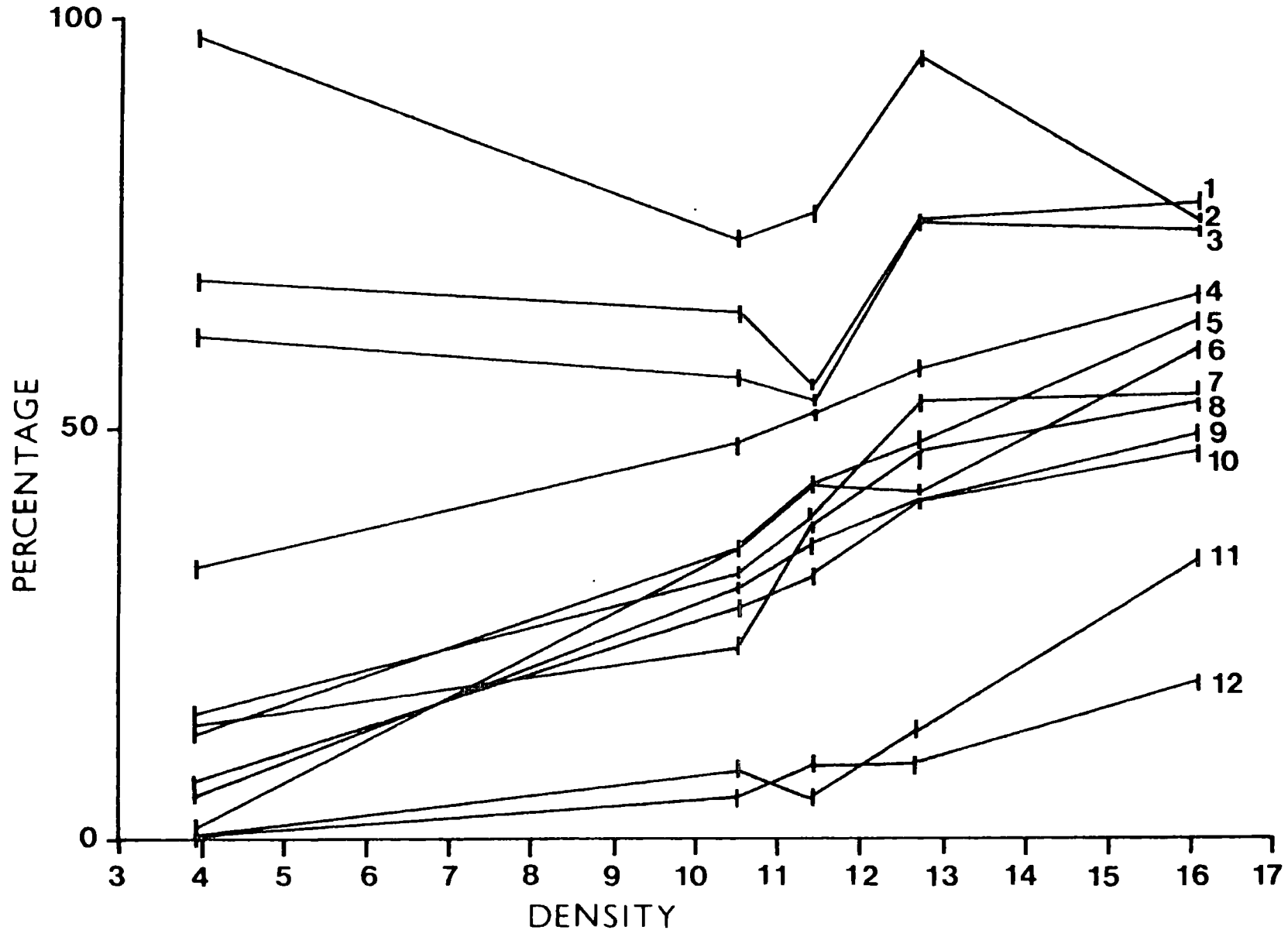
Colony	First date on which 10%, 20%, 30% and 40% of the sites were occupied in 1975 (1 January = 1)			
	10%	20%	30%	40%
SF	7	10	10	17
WF	7	7	30	30
NC	10	17	27	27
GC	20	20	27	27
SC2	27	30	30	34
FSC	27	27	30	30
MVB	27	27	27	30

Figure 6 The relationship between the percentage of sites occupied and colony mean density of the five main study areas for eleven dates in January and February and one date in April 1976. The high density colonies had a higher percentage of sites occupied on each day during the reoccupation phase. As the season progressed the differences became less marked.

(Dates : 1 = 24.2 2 = 1.4 3 = 17.2 4 = 13.2

5 = 23.1 6 = 10.2 7 = 13.1 8 = 27.1

9 = 8.1 10 = 15.1 11 = 20.1 12 = 5.1)


100
50
0
PERCENTAGE
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
DENSITY
1
2
3
4
5
6
7
8
9
10
11
12

one date in April in 1976, shows that the percentage of sites occupied on each day increases with nest density. As none of these colonies is steadily increasing, it seems unlikely that these differences are due to differences in the age structure. It should be remembered that the differences found here in the dates of return to the different colonies are less marked than those reported by Coulson and White (1956). It may be that mortality in low density peripheral areas is higher than in the high density areas (Coulson 1968) but if this were to explain the observed effect, a linear relationship between annual mortality rate and nesting density would be necessary. Evidence for or against this is lacking.

The North Colony was divided into five areas according to the topography of the cliff, and the return in 1975 and 1976 was recorded (Table 8). The order of return did not follow that of mean density of each area. The peripheral areas (1 and 5), which were both increasing and may be expected to have had a high proportion of young birds nesting in them, were the latest areas to be reoccupied. The densest area, and the most stable in numbers, was, in each case, the first area to be re-occupied (not the initial area of cliff colonisation i.e. area 3). These data indicate that both the number of young birds in the colony and also the nesting density are important in influencing the date of return to each area.

As the percentage of sites occupied increases through the season, the time spent by individuals at the colony daily increases. By the time that a quarter of the sites are occupied, the birds arrive at the colony shortly before sunrise and depart around sunset: the birds leave in panic flights and fly straight out to sea. The numbers of sites occupied increases during the day, reaching a peak in the late afternoon. By the time that fifty percent of the sites are regularly occupied, the birds remain at the colony until several hours after sunset, and only observations

Table 8. The order of recolonisation of five areas of the North Colony at the start of the 1975 and 1976 seasons did not follow that of mean nesting density. The peripheral areas (1 and 5), which were both increasing and may be expected to have had a high proportion of young birds nesting in them, were the latest areas to be reoccupied. The densest area, which was stable in numbers, was in each year the first to be reoccupied. The original area of cliff colonisation was area 3. The magnitude of the differences in the dates of return to the areas of the colony are shown.

North Colony Areas	Nest Count 1975	Order of Recolonisation 1975	1976	0-5' Mean density	Percentage change in nests 74.75	75.76
1	142	4	4	10.5	+18	+20
2	681	1	1	11.2	+ 5	- 3
3	214	3	3	8.3	+10	- 7
4	186	2	2	4.7	- 5	+ 3
5	54	5	5	1.3	+14	-20

First date on which 10%, 20%, 30% and 40% of the sites were occupied (1975 and 1976) (1 January = 1)

	1975				1976			
Area	10%	20%	30%	40%	10%	20%	30%	40%
1	20	27	30	30	8	13	23	41
2	17	17	27	27	8	8	8	13
3	17	20	27	27	8	8	23	44
4	10	27	27	27	8	8	8	13
5	20	27	27	47	13	27	47	47

in the dark showed that the colonies were in fact vacated at night. Counts of birds present at night were impossible, although their presence or absence was detected, using a strong flashlight. The colonies were vacated daily up until about two weeks before egg laying. As the percentage of sites occupied increases through the season, the percentage of sites occupied by pairs increases (Figure 7): thirty percent of the occupied sites are occupied by pairs only by the time that forty five percent of the sites are occupied. As the pair bonds stabilise and the season progresses, pairs sperd less time together. After the eggs are laid there is a marked decline in the time that pairs spend together, and thus a reduction in the percentage of occupied sites occupied by pairs (Figure 11).

The five main study areas were divided into twenty five units, each having at least twenty nests, and the mean date of return in 1976 of each unit was plotted against the mean density of each unit (Figure 8). The significant negative relationship ($r_{23} = -0.75$, $b = -0.42 \pm 0.077$, $c = +23.4$, $p < 0.001$) again shows the importance of colony density in determining the date of return. From this relationship it can be predicted that for an increase of one pair nesting within a five feet radius of any bird, that bird will return two and a half days earlier in the following breeding season. Nesting density in the ensuing breeding season can not have a direct effect on the date of return to the colony. If density does have an effect, and the evidence strongly suggests that it does, it is not restricted to its effect on any one season, but affects the following year, in that a high nesting density in one year gives rise to an advanced, earlier, date of return to the colony at the start of the following breeding season.

Figure 7 The percentage of occupied sites occupied by pairs against the percentage of sites occupied, during the reoccupation phase (January to April), for the five main study areas. As the percentage of sites occupied increases through the reoccupation phase, the percentage of sites occupied by pairs increases. Thirty per cent of the occupied sites are occupied by pairs only by the time that forty five per cent of the sites are occupied.

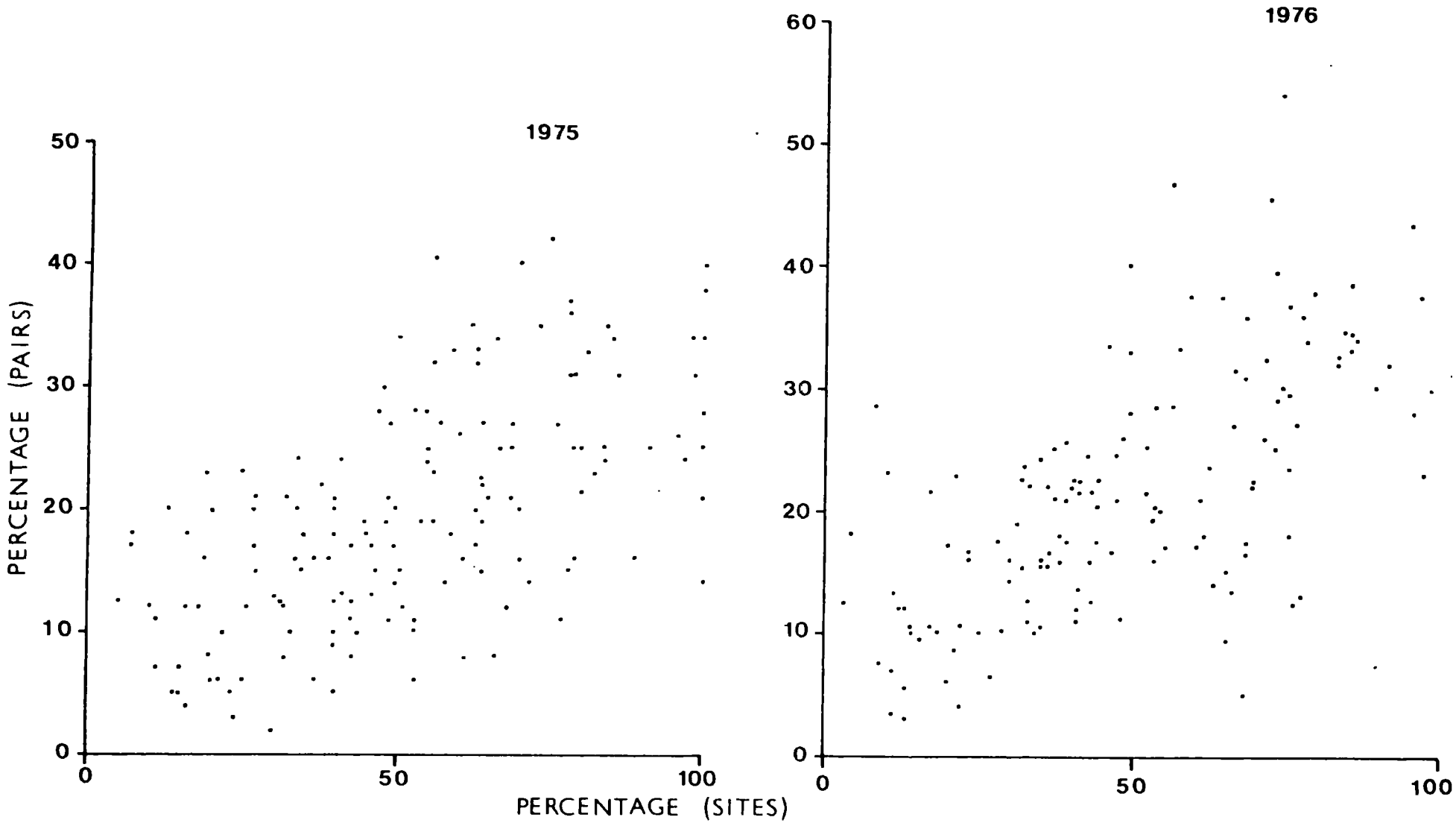
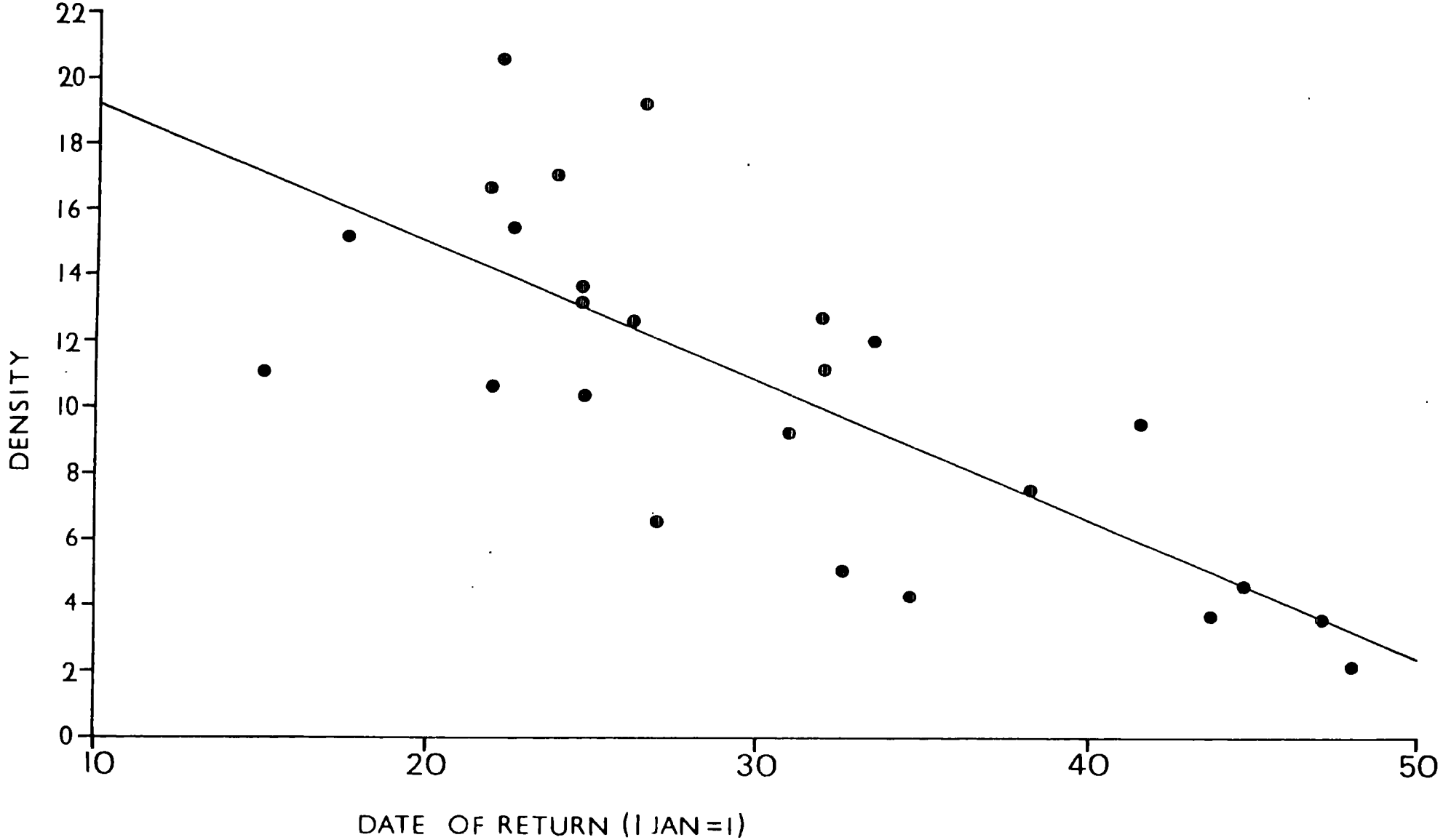

1975
1976
PERCENTAGE (PAIRS)
PERCENTAGE (SITES)
0
10
20
30
40
50
60
0
50
100

Figure 8 The five main study areas were divided into twenty five units, each having at least twenty nests, and the mean date of return to each area in 1976 plotted against the mean nesting density of each unit (nests within a 5' radius). Birds breeding in high density areas return to the colony earlier at the start of the following season. The significant relationship ($r_{23} = -0.75$, $p < 0.001$) is described by the regression equation:

$$y = -0.42x + 23.4$$


22
20
18
16
14
12
10
8
6
4
2
0
DENSITY
10
20
30
40
50
DATE OF RETURN (1 JAN = 1)

The effect of wind speed

Wind speed was the sole environmental factor found to have a marked effect on the number of birds present on consecutive days. On days when the wind speed was above eleven knots (12.7 mph) the numbers of birds were dramatically reduced. Counts from such dates (during the period of reoccupation of the colonies) were paired with those made on the next or previous visit, when similar numbers of birds could be expected. These data were graphed against the mean daily wind speed (Figure 9).

Similarly, the effect of wind speed on the numbers of pairs present is shown in Figure 10. It is seen from these figures that on dates when the numbers of sites occupied and the numbers of pairs present are reduced, the wind speed is greater than eleven knots. Increases in wind speed firstly cause a drop in the number of pairs present, and secondly in the number of sites occupied. As there is considerable competition for nest sites it is an obvious advantage for one bird of a pair to remain at the nest site when other birds are attempting to find sites. As the season progresses the effect of wind speed decreases, and by May has little effect on the presence of breeding birds. Increases in wind speed at this time do cause reductions in the number of young prospecting birds.

Individual variation in the date of return to the colony at the start of the season

As kittiwakes show marked nest site tenacity, and older birds return to the colony earlier, a positive relationship between the dates of arrival of individuals in successive years may be expected. The correlation coefficient for the dates of arrival to all sites in the main

Figure 9 The effect of wind speed on the percentage of sites occupied in the main study areas, during the period of reoccupation (14.1.75 to 11.4.75: 15.1.76 to 10.2.76). Counts from days on which the wind speed was above eleven knots (12.7 mph) were paired with those taken on the subsequent, or previous, visit, when similar numbers of birds could be expected. The percentage of sites occupied on each day was plotted against the mean daily wind speed. On days when the wind speed was above eleven knots the percentage of sites occupied was reduced.

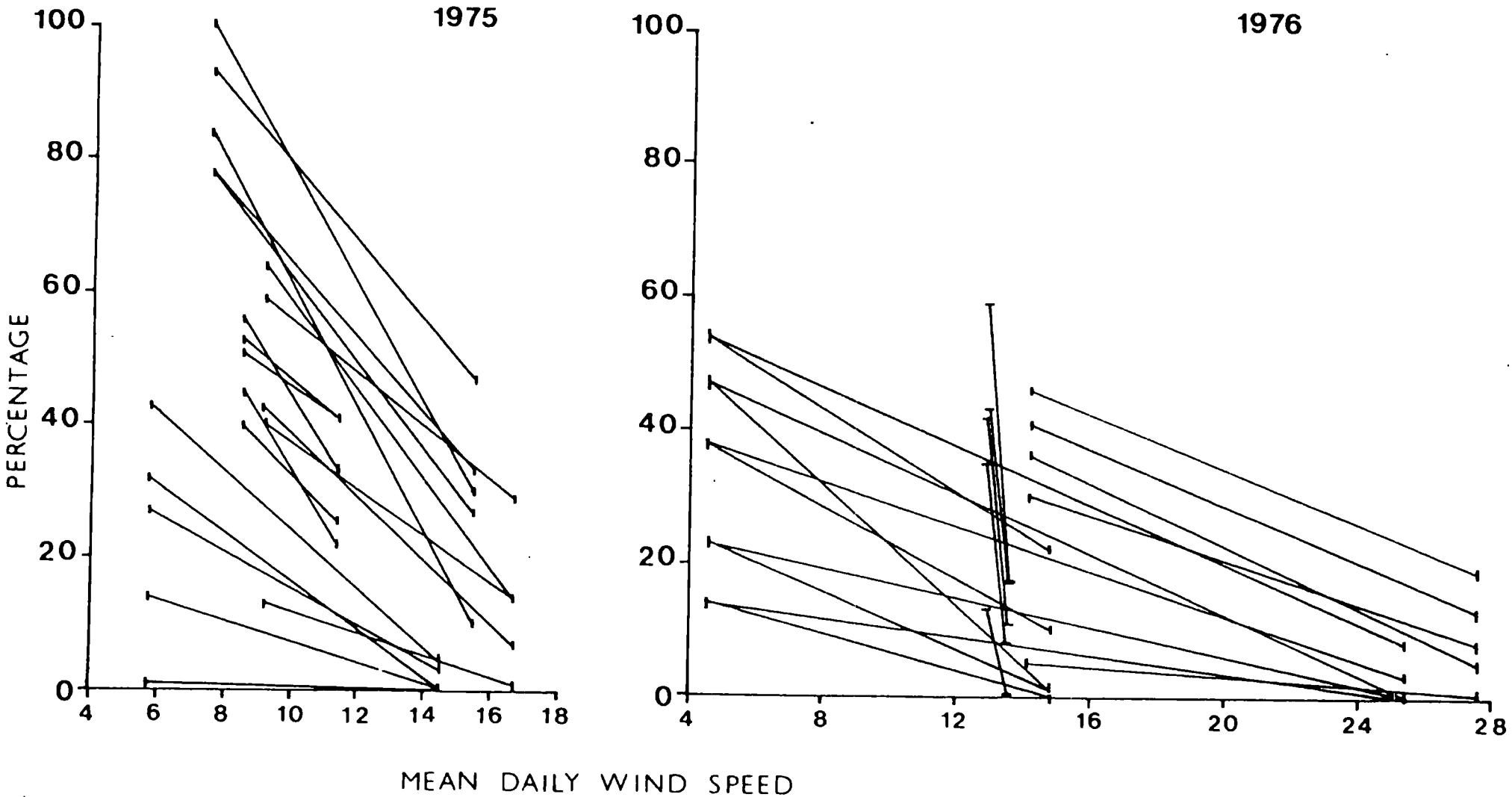
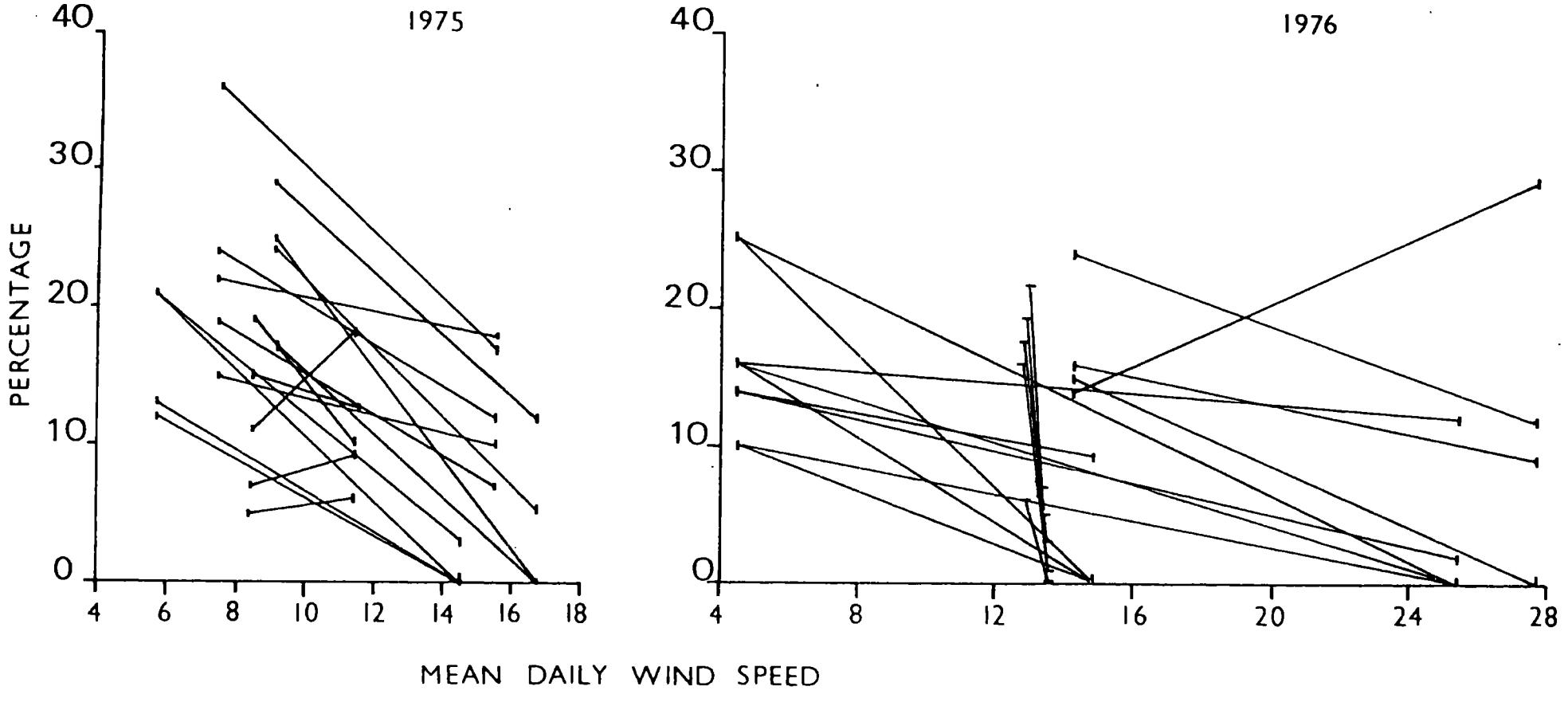

1975
1976
100
80
60
40
20
0
PERCENTAGE
4
6
8
10
12
14
16
18
20
24
28
MEAN DAILY WIND SPEED

Figure 10 The effect of wind speed on the percentage of occupied sites occupied by pairs in the main study areas, during the period of reoccupation (14.1.75 to 11.4.75 : 15.1.76 to 10.2.76). Counts from days on which the wind speed was above eleven knots (12.7 mph) were paired with those taken on the subsequent or previous visit (when a similar percentage of occupied sites occupied by pairs could be expected) and these data graphed against mean daily wind speed. On days when the wind speed was above eleven knots the percentage of pairs present was reduced.


1975
1976
PERCENTAGE
0
10
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40
4
6
8
10
12
14
16
18
20
24
28
MEAN DAILY WIND SPEED

study areas for 1975 and 1976 was calculated (r_{817} = +0.44, b = +0.24 ± 0.017, $p < 0.001$). Similarly, the correlation between the date of departure in 1975 and the date of arrival in 1976 was calculated (r_{817} = -0.33, b = -0.24 ± 0.024, $p < 0.001$). Birds which are early in arriving back at the colony at the start of the season are consistently early; moreover, they vacated the colony later at the end of the previous season. The relationship between the date of departure and the date of arrival in the following year predicts that any bird will return four days earlier in the next breeding season for each additional day that it remained at the colony. Table 9 shows the correlation coefficients for each main study area where the situation is seen to be similar. The relationship between the dates of arrival in successive years is thus not only a function of colony density, but points to the importance of individual variation.

Attendance

The attendance at all colonies throughout 1974 and 1975 was recorded. The most striking differences between the colonies were the percentages of young prospecting birds present. Proportionately more such birds were present in the low density colonies (Table 10), indicating that in these colonies potential nest sites were available.

The percentage of sites occupied by pairs was highest during the pre-egg laying period when pair formation and courtship take place. After egg laying, the number of sites occupied by pairs drops dramatically. After the chicks have fledged, and before the vacation of the colony by breeding birds, there is a resurgence of courtship behaviour, when the percentage of sites occupied by pairs shows a distinct peak.

Figure 11, the annual occupation of the South Face colony in 1975, shows these points.

The vacation of the colony at the end of the season

The vacation of the colonies is similar to the reoccupation, but in reverse order. The birds arrive early in the day, and as the daily time of departure advances the pattern of panic flights becomes more frequent, involving a greater proportion of the birds. The differences between the colonies in the dates of departure are less marked than those during the reoccupation phase (Figure 12).

Table 9 The correlation coefficient describing the relationship between the date of departure and the date of return to the colony, and the correlation coefficient describing the relationship between the dates of return to the colony in successive years, for individual nest sites in each main study area. Birds which are early in arriving back at the colony at the start of the season are consistently early. Moreover, those birds that arrive early in the season vacated the colony later at the end of the previous season.

Colony	r1	N	p	r2	N	p
SFa	-0.35	116	<0.001	+0.22	116	<0.02
WF	-0.43	267	<0.001	+0.35	267	<0.001
NCn	-0.28	130	<0.01	+0.47	130	<0.001
NCo	-0.43	156	<0.001	+0.26	156	<0.001
SCl	-0.14	150	NS	+0,34	150	<0.001
Total	-0.33	819	<0.001	+0.44	819	<0.001

r1 = the correlation coefficient between the date of departure from the colony in 1975 and the date of arrival at the colony in 1976

r2 = the correlation coefficient between the dates of arrival at the colony at the start of the season in 1975 and 1976

The correlation coefficients for each main study area and for their total are shown.

N = sample size

Table 10 In 1975, on twelve of the dates on which counts were made the total number of sites occupied was above the total number of nest sites used in that year. The mean value of the percentage of sites occupied in each colony on such dates is shown. In the low density colonies the percentages of sites occupied were higher than those in the high density colonies, indicating that in the low density colonies potential nest sites were available.

Colony	Mean density 0-5'	Mean percentage of sites occupied
SF	16.4	112.0
NC (area 1)	10.5	121.4
WF	13.2	95.3
NC (area 3)	8.3	98.5
SC1	2.2	125.9
FSC	3.1	127.6
SC2	2.2	132.7
MVB	3.4	124.5
GC	4.3	135.5

Figure 11 The percentage of sites occupied, and the percentage of occupied sites occupied by pairs, in the South Face colony in 1975. After egg laying the percentage occupied by pairs drops dramatically, and increases after fledging. Non-breeding birds arrive after the breeding birds during May and June, and vacate the colony before the breeding pairs at the end of the season. Solid dots and heavy lines represent the percentage of sites occupied: broken lines and open circles represent the percentage of occupied sites occupied by pairs. The mean laying date is indicated by an arrow.

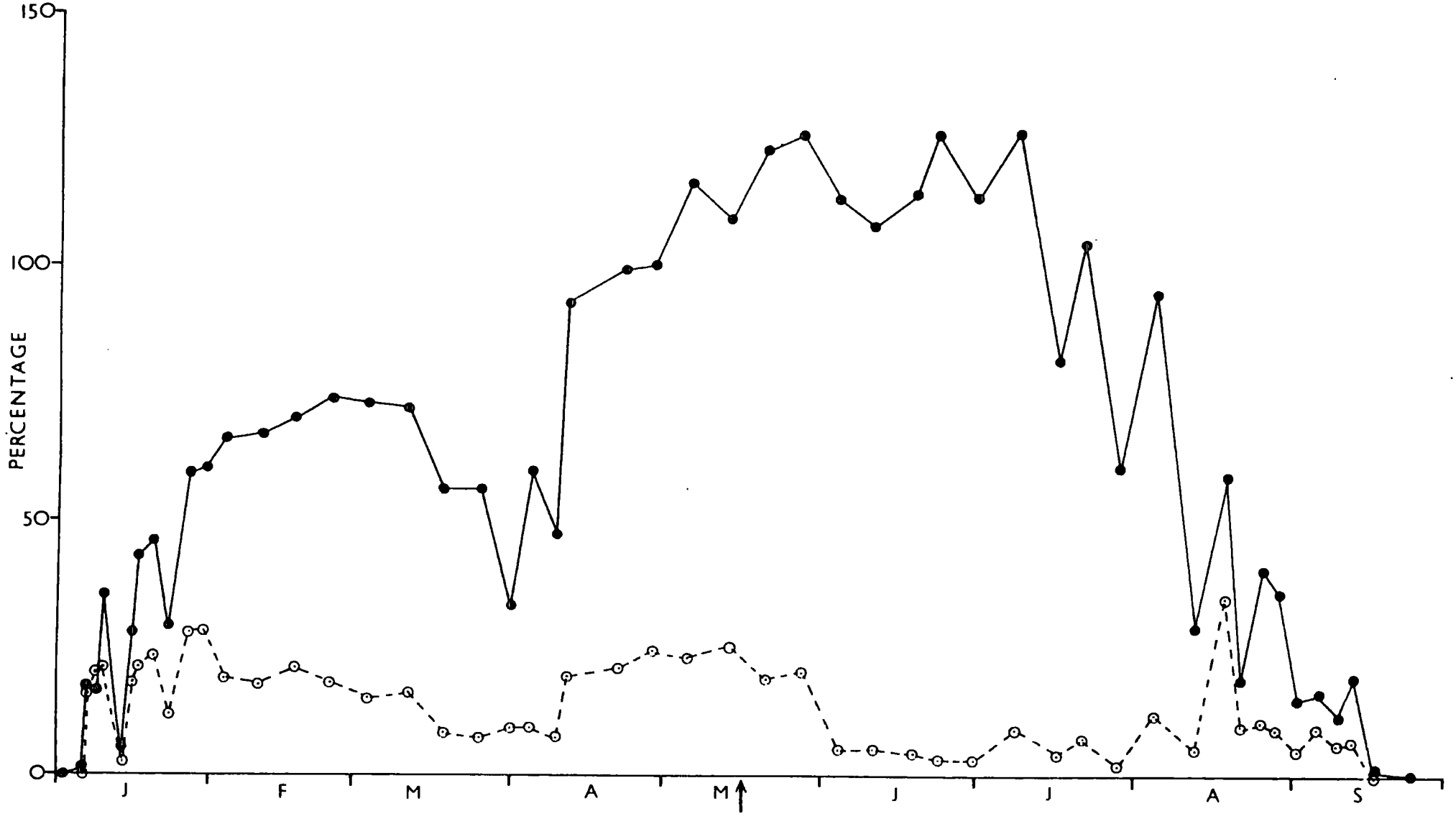
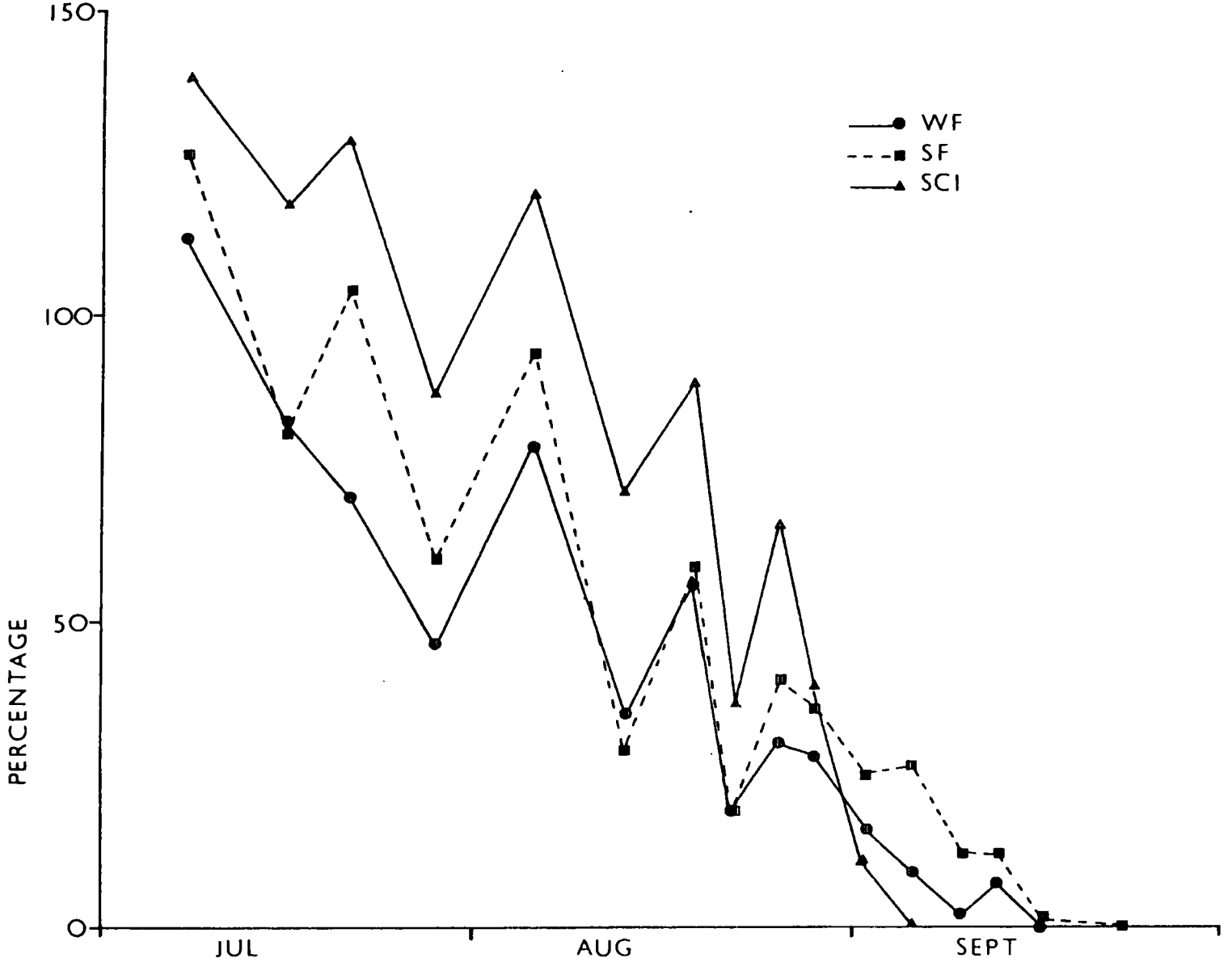

150
100
50
0
PERCENTAGE
J
F
M
A
M
J
J
A
S

Figure 12 The vacation of 3 colonies in 1975. The vacation of the colonies is similar to the reoccupation, but in reverse order. The differences between the colonies in the dates of departure are less marked than those during the reoccupation phase.


150
100
50
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PERCENTAGE
JUL
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SEPT
WF
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SCI

PLUMAGE CHANGES

Adult kittiwakes in winter plumage have a dark grey neck band which is lost prior to breeding. Many of the birds return to the colonies with this dark neck band still present. It is accepted for many bird species that such plumage changes are hormonally controlled and relate to the reproductive condition of the bird (Boss 1943, Payne 1972). This is likely to be true for the kittiwake where reproduction and moulting are in phase. The distribution of the light and dark-headed birds in the different colonies was thus investigated during the reoccupation period. Counts of light and dark-headed birds in each colony were made in 1975 and 1976. Only birds which had lost all the dark plumage were recorded as light-headed. The distance over which observations were made, made more detailed classification into three or four stages unreliable. The numbers of light and dark-headed birds in a sample of at least one hundred birds in each colony were counted when possible; counts were made twice weekly.

Table 11 shows that, in both 1975 and 1976, the percentages of light-headed birds during the initial period of reoccupation of each colony were different: the initial proportions of dark-headed birds were higher in the low density colonies. In 1976, when the percentage of light-headed birds was only 25%, the high density colonies were regularly occupied. However, only by the time that the percentage of light-headed birds reached 50% in the low density colonies were the colonies regularly occupied. This indicates that the plumage changes, although they may reflect hormonal changes in the bird, are not indicative of the full complement of factors governing the date of return to the colonies. On days when few birds were present, higher proportions of light-headed birds were present (e.g. 20.1.76), which does point to the importance of plumage changes as an indicator of the drive to remain on the nest site.

Table 11 The percentage of birds in the different colonies in breeding plumage (with light heads) during the reoccupation phase in 1975 and 1976. The higher density colonies have a greater percentage of birds in breeding plumage on any day

Colony	Date 1975						Date 1976								Colony density
	17 Jan	20 Jan	23 Jan	30 Jan	3 Feb	10 Feb	6 Jan	8 Jan	13 Jan	15 Jan	20 Jan	23 Jan	27 Jan	30 Jan	
SF	66	66	78	94	89	90	34	31	49	48	65	56	74	85	16.4
WF	61	67	86	69	81	84	29	28	33	47	50	54	60	100	13.2
NC (area 1)	44	57	80	61	68	92	*	36	42	56	*	53	76	Ø	10.5
NC (area 3)	*	36	73	54	62	79	*	23	27	28	69	47	57	Ø	8.3
GC	49	49	55	64	53	84	*	26	26	38	46	53	59	*	4.3
MVB	Ø	*	Ø	59	45	74	Ø	*	16	Ø	*	*	50	Ø	3.4
SC1	*	Ø	*	50	51	63	*	Ø	13	*	Ø	*	61	Ø	2.2
SC2	Ø	46	*	51	51	64	Ø	*	9	Ø	Ø	*	41	Ø	2.2

Ø no birds present

* too few birds counted for analysis (less than 20)

The percentages of birds in light plumage on 30.1.75 and 13.1.76 were plotted against colony mean nesting density (Figure 13). The positive correlations are significant (1975 $r_6 = +0.82$, $b = +2.16 \pm 0.45$, $p < 0.05$: 1976 $r_6 = +0.93$, $b = +2.41 \pm 0.34$, $p < 0.01$). During the reoccupation phase, higher percentages of light-headed birds could be expected in high density colonies on any day.

During the initial phase of reoccupation, when only the denser colonies were occupied, no differences in the proportions of light-headed birds in the colonies were observed. However, as the season progressed and the lower density colonies were reoccupied, the differences between the colonies became more marked and significant (Tables 12 and 13). In each case the expected proportion of light-headed birds was lower than the observed proportion in the high density colonies. As the proportion of light-headed birds neared unity the differences between the colonies became insignificant.

The difference between the optimum number and observed number of birds present in the colonies was calculated and expressed as a proportion of the optimum number of birds present. This was graphed against the observed minus the expected percentage of birds with light heads (Figure 14). On days when the number of birds present in the colonies was below the optimum number, the percentage of birds with light plumage was higher than the expected percentage. This indicates that those birds with light heads have a stronger urge to occupy the breeding sites, and upholds the assumption that the birds with light plumage are hormonally more advanced in terms of breeding condition. As there is no difference in the date of return to the nest site of males and females, and as in many bird species the gonads of the male develop earlier in the season than those of the female, a difference between the sexes in the proportion of birds with light plumage could be expected. As there was no reliable way of sexing individuals at the Marsden colonies, possible differences could not be investigated.

Figure 13
(after Table 12)

The percentage of birds in breeding plumage (with light heads) in eight colonies on 30.1.75 and 13.1.76 against the colony mean density (nests within a radius of five feet). The high density colonies have a higher percentage of birds in breeding plumage (1975 $r_6 = +0.82$, $p < 0.05$: 1976 $r_6 = +0.93$, $p < 0.01$). The regression equations are:

1975 $y = +2.16x + 46.4$

1976 $y = +2.41x + 8.65$

Table 12. 1975. The χ^2 test for homogeneity in the different colonies in the proportions of birds with light plumage. During the initial phase of reoccupation there were significant differences between the colonies. However, as the season progressed, and the proportion of birds with light heads neared unity, the differences between the colonies became insignificant.

Date 1975	SF	WF	NF	NC	GC	SC1	B1+B2+SC2	$\Sigma\chi^2$	EXP LIGHT	d.f.	p
17.1	6.59	4.27	0.31	7.39	0.56		1.57	20.69	0.55	5	< 0.001
20.1	13.25	6.41	5.76	2.49	0.55		3.64	32.10	0.53	6	< 0.001
23.1	0.62	1.99	1.47	0.88	5.19			10.15	0.73	4	< 0.05
30.1	59.22	0.04	0.07	5.48	0.63	5.11	7.91	78.46	0.68	6	< 0.001
3.2	30.66	6.50	1.01	1.39	13.62	7.74	12.99	73.91	0.68	6	< 0.001
10.2	8.01	1.25	3.23	3.34	1.40	17.96	30.17	65.36	0.80	6	< 0.001
17.2			0.46	0.01	1.51	0.19	0.64	2.81	0.90	4	N.S.
24.2	0.83	10.62			⊢3.31⊣		0.43	15.08	0.92	3	< 0.01
3.3	0.21	⊢0.06⊣		0.06	⊢0.87⊣		0.47	1.67	0.96	4	N.S.

χ^2 values for each colony are shown. In certain cases the data from two adjacent colonies have been summed because of the small sample sizes e.g. GC and SC1 on 24.2.75.

EXP LIGHT = the expected proportion of birds in light plumage.

d.f. = degrees of freedom.

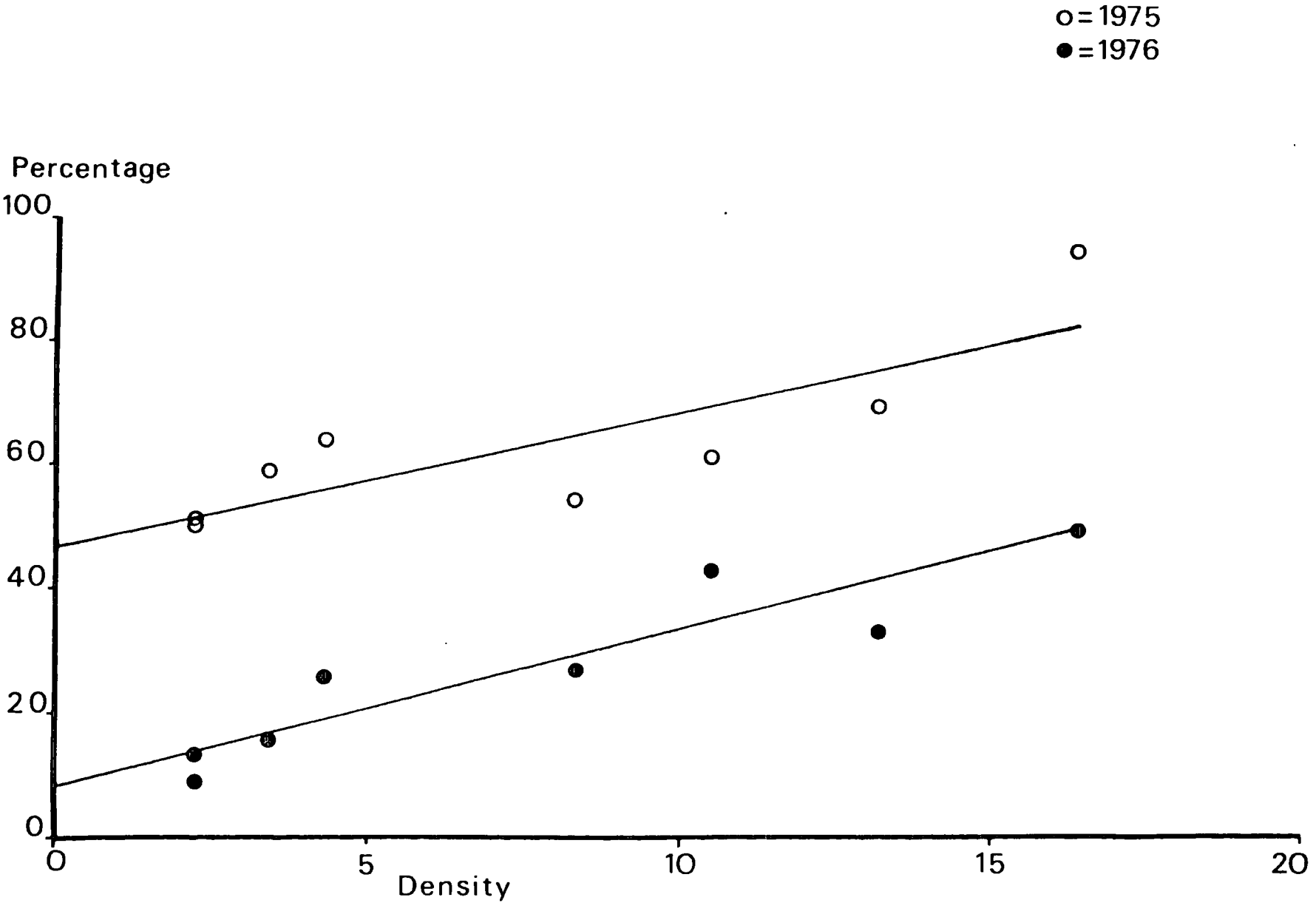
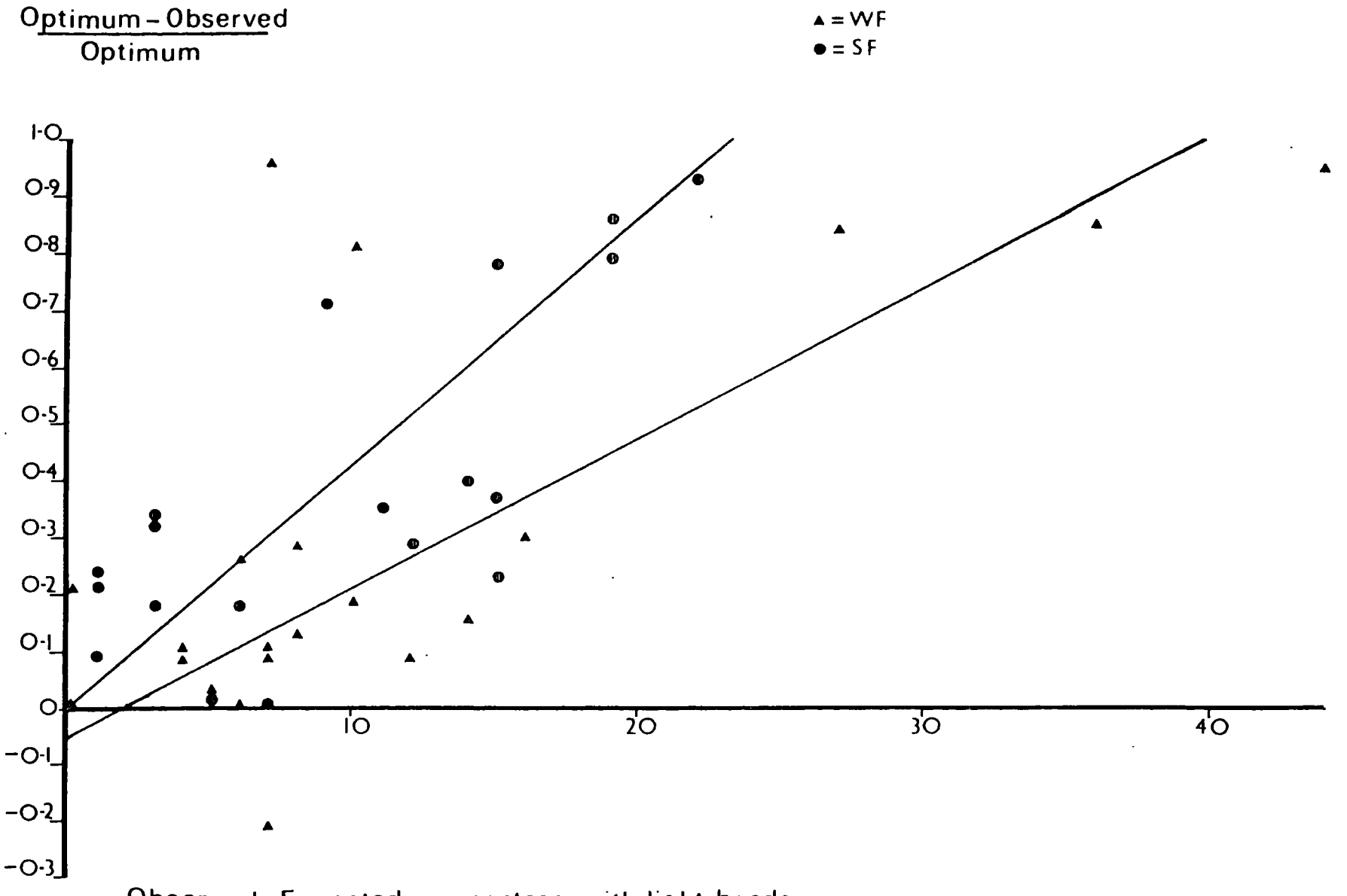

o = 1975
● = 1976
Percentage
100
80
60
40
20
0
0
5
10
15
20
Density

Table 13. 1976. The χ^2 test for homogeneity in the different colonies in the proportions of birds with light plumage. During the initial phase of reoccupation when only the denser colonies were occupied no differences in the proportions of light-headed birds in the colonies were observed. As the season progressed, and the lower density colonies were reoccupied, the differences between the colonies became more marked. As the expected proportion of light-headed birds neared unity, the numbers of light-headed birds in each colony were too low for statistical analysis.

Date 1976	SF	WF	NC	GC	SC1	MVB	B1+B2+SC2	FSC	$\Sigma\chi^2$	EXP LIGHT	d.f.	p
5.1	0.01	0.04							0.05	0.29	1	N.S.
8.1	1.15	0.00	0.39	0.23					1.77	0.28	3	N.S.
13.1	37.33	0.02	5.90	3.49	⊢10.62⊣				57.36	0.33	4	< 0.001
15.1	1.73	0.01	0.65	0.55					2.94	0.40	3	N.S.
20.1	1.00		0.20	3.91					5.11	0.60	2	N.S.
23.1	0.36	0.02	0.18	0.00					0.56	0.54	3	N.S.
27.1	12.26	0.03	3.09	0.08					15.46	0.61	3	< 0.01
6.2	0.14	0.11	0.04						0.29	0.90	2	N.S.
10.2	11.52	1.84	1.44	0.53	0.03		5.37	6.51	27.24	0.79	6	< 0.001
13.2	10.64	0.01	0.29	0.23	2.37		2.27	0.81	16.62	0.79	6	< 0.05
17.2	1.37	0.48	10.56	9.64	10.40	8.24	15.38	7.03	63.10	0.78	7	< 0.001
20.2	7.07	5.59	6.22	3.82	2.91	6.63	24.86	24.53	81.63	0.86	7	< 0.001
24.2	2.28	0.02	0.52	2.84	0.08	3.45	1.24	5.28	15.71	0.93	7	< 0.05
27.2	0.87	0.15	1.78	1.05	0.35	0.11	4.20	11.14	19.65	0.89	7	< 0.01
2.3	0.24	0.30	0.13	1.63	1.23	1.52	0.06	9.33	14.44	0.92	7	< 0.05

χ^2 values for each colony are shown. On 8.1.76 the data from SC1 and MVB were summed because of the small sample sizes.
EXP LIGHT = the expected proportion of birds in light plumage
d.f. = degrees of freedom.

Figure 14. 1976. The differences between the optimum number and observed number of birds present in the South Face and West Face colonies were calculated and expressed as a proportion of the optimum number of birds present. They were graphed against the observed minus the expected percentage of birds with light heads. On days when the number of birds present in the colonies was below the optimum number, the percentage of birds with light heads was higher than the expected percentage.


Optimum – Observed
Optimum
▲ = WF
● = SF
1·0
0·9
0·8
0·7
0·6
0·5
0·4
0·3
0·2
0·1
0
−0·1
−0·2
−0·3
10
20
30
40
Observed – Expected percentage with light heads

THE DISTANCE OF REACTION

Much evidence has been presented to show that variation in day length and other environmental factors affect the time and rate of gonad development, and thus the timing of the breeding season in birds. Gonad development and their hormone secretion occur under the influence of stimulating hormones from the pituitary. Investigations into whether courtship behaviour by males stimulates the secretion of gonad stimulating hormones by the pituitary of females have indicated that this is so (Burger 1942, Polikarpova 1940, Matthews 1939, Lehrman 1959, Lehrman, Brody and Wortis 1961, Lehrman and Friedman 1969). Moreover, there is some evidence that stimuli from the female have an effect on male gonads (Burger 1953). Further studies have indicated the importance of a number of individuals producing a stimulatory effect on gonad development of members of a pair (Vaugien 1951), and on nest building activity (Collias, Victoria and Shallenberger 1971).

As the kittiwake is unable to breed successfully in isolation, the presence of individuals other than the mate presumably provides an exteroceptive stimulus which acts on the pituitary. In the present study the role of auditory and visual stimulation from individuals other than the mate was investigated. There is no evidence of tactile stimulation between individuals, other than between mates.

When a kittiwake returns to the nest the mates greet each other in a characteristic way, the kittiwaking ceremony, which is a complex display of bowing, calling and choking. This ceremony often produces reaction in neighbouring pairs, and a less marked response in birds which are, at the same time, on their nest site. The infectious nature of the response was investigated during the pre-egg laying phase using multiple focal animal sampling (Altmann 1974). This method was practicable because it was possible to keep every member in the group under continuous

observation during the sample period, the observation conditions were good, the behaviour being studied was attention-attracting because vocal, and did not occur too frequently to confuse its recording. Observations were made on the North Colony New area, NCn, and the South Colony one, SCl: records were taken of all landings resulting in the reunion of a pair, in each sample period of five minutes. The distance, direction and reaction of all pairs within a five feet radius of the reunited pair were recorded. Similarly, the effect on single birds, and on pairs, of single birds landing on empty nest sites, and the effect of reunited pairs on single birds, were recorded.

Table 14 shows the response of single birds to birds landing on empty sites and choking, and to reunited pairs kittiwaking. Single birds did not 'kittiwake', but responded by choking, a less intense response. The proportion of birds choking was greater in response to pairs kittiwaking than singles choking, and is significantly greater at 2, 3 and 4 feet ($p<0.05$ at 2': $p<0.001$ at 3': $p<0.05$ at 4').

The proportion of pairs responding to single birds and to pairs is shown in Table 15. The strongest response is by pairs which are stimulated to kittiwake by reunited pairs kittiwaking: a higher proportion of birds react than react to single birds, and the distance over which pairs respond is greater. Although the kittiwake has an extensive range of sexual behaviour patterns, it is only the pair greeting ceremony which is seen to have a marked influence on neighbouring pairs, and the infectious nature of this ceremony is usually restricted to a radius of five feet from the reunited pair. An examination of the distance over which pairs show a response to the greeting ceremony in the North Colony New area and the South Colony One area is shown in Figure 15. There is clearly a rapid decrease in the proportion of pairs which respond as distance increases, with the most frequent response occurring in birds

Table 14 An analysis of the distance over which single birds will respond to other birds

Proportion of Single birds choking in response to birds landing on empty sites and choking

Distance (feet)	1	2	3	4	5
Proportion choking	.52	.21	.03	.03	.13
N	31	67	61	66	69

Proportion of Single birds choking in response to reunited pairs kittiwaking

Distance (feet)	1	2	3	4	5
Proportion choking	.51	.34	.27	.13	.10
N	59	140	131	135	200

Table 15 An analysis of the distance over which pairs will respond to other birds

Proportion of Pairs kittiwaking in response to birds landing on empty nest sites and choking

Distance (feet)	1	2	3	4	5
Proportion kittiwaking	.33	.06	0	0	0
N	6	45	49	49	30

Proportion of Pairs choking in response to birds landing on empty sites and choking

Distance (feet)	1	2	3	4	5
Proportion choking	.25	.02	.04	.02	0
N	4	42	49	49	30

Proportion of Pairs kittiwaking in response to reunited pairs kittiwaking

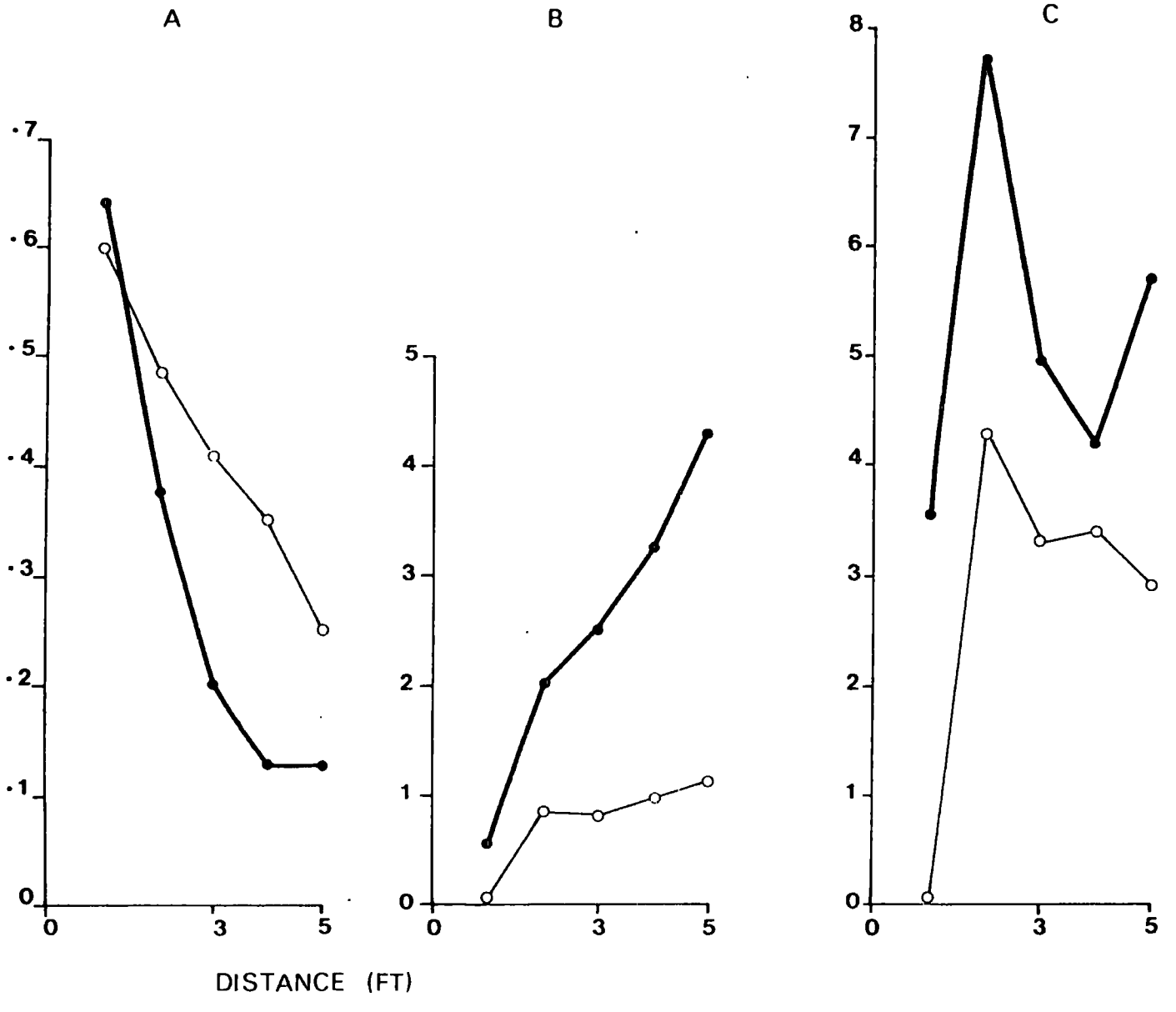
Distance (feet)	1	2	3	4	5
Proportion kittiwaking	.64	.37	.23	.17	.15
N	128	497	451	448	623

Figure 15 An examination of the distance over which pairs show a response to a greeting ceremony during the pre-egg laying phase. Two colonies of different density are represented. Solid dots and heavy lines represent the dense colony (NCn): open circles and thin lines represent the sparse colony (SC1).

A. shows the probability of a pair responding to a greeting ceremony at successive distances from it.

B. shows the mean number of nests present in the colony. These data are obtained from photographs by calculating the mean number of nests at each distance.

C. shows the mean number of pairs responding to a greeting ceremony at successive distances: this is the product of A and B.


A
B
C
·7
·6
·5
·4
·3
·2
·1
0
5
4
3
2
1
0
8
7
6
5
4
3
2
1
0
0
3
5
DISTANCE (FT)

with nests immediately adjacent. In the less dense colony (SC1) the response rate is significantly higher at distances greater than two feet ($p<0.001$: $p<0.001$: $p<0.01$). It appears that there is a compensating effect: the birds nesting at low density respond more readily to greeting ceremonies which take place at greater distances from them. Although the general activity in the two colonies was equivalent in terms of the number of landings in each sample period, in the South Colony One (SC1) 56% of the sites on which pairs were reunited had no other pairs within a five feet radius (cf. 32% in the North Colony New area, NCn). Spontaneous kittiwaking, which was not obviously triggered by the behaviour of neighbours, occurred in both colonies. It was infrequent, and there was no significant difference in its occurrence in the two colonies.

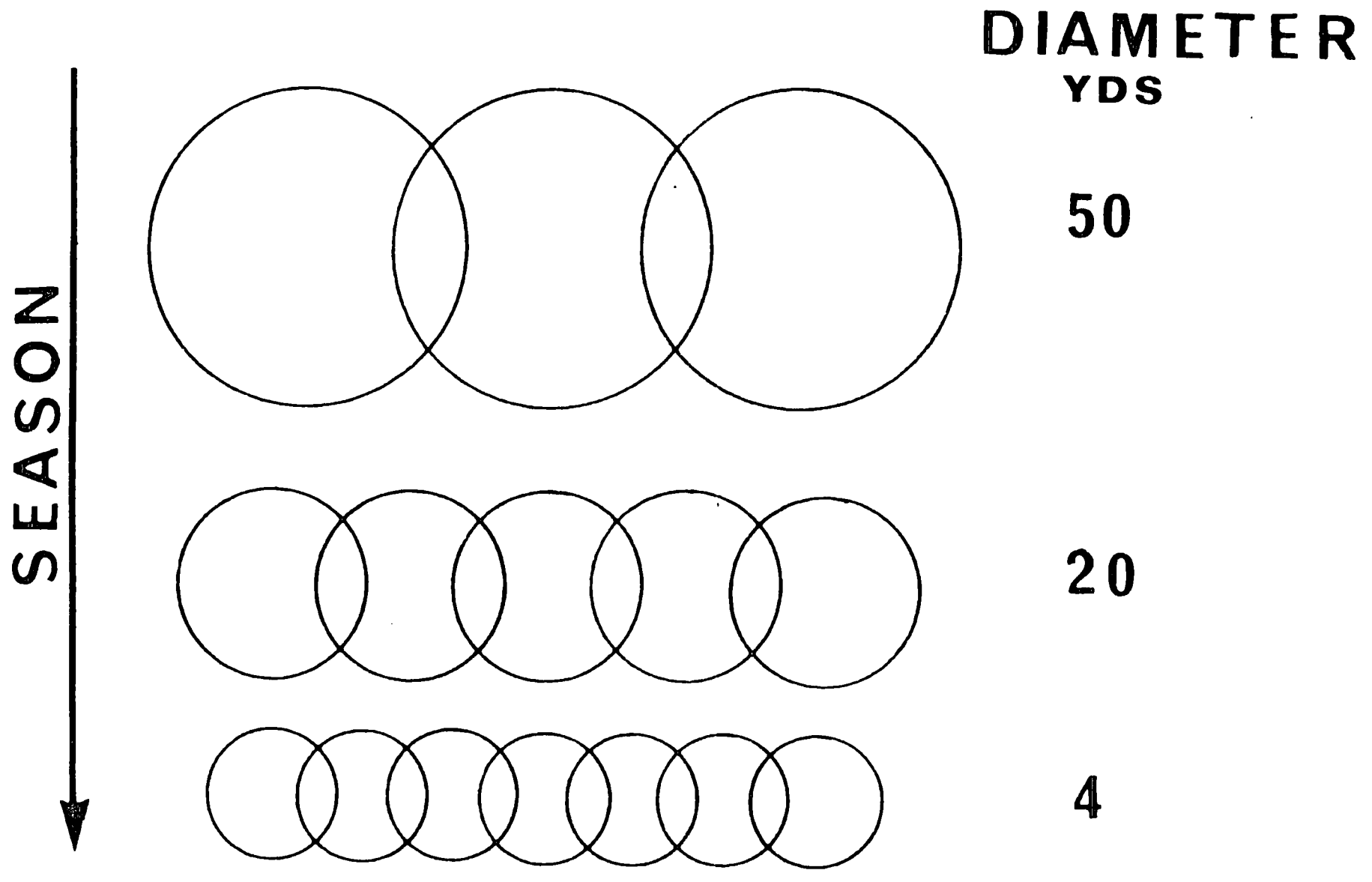
The number of nests at successive distances from an individual nest tends to increase with distance (Figure 15). This does not follow the expected trend, based on the geometric relationship of the area of the concentric circles (i.e. 1:3:5:7:9). The nests are not randomly distributed because kittiwakes can only nest where there are suitable ledges, and these are determined by the geological structure of the cliff face. By multiplying the probability of response by the number of nests at each distance the mean number of pairs influenced at progressive distances is obtained. This also indicates the distance from which each pair receives the maximum stimulation which, from the data presented, is at two feet in both the low and high density colonies. No differences were found in the response rate in nests at different directions from the central pair.

There are three activities in which there are clear responses in neighbouring individuals. In panic flights, although there is considerable variation in the distance over which birds are influenced, on average, birds are affected over a radius of twenty five yards.

Nest building is often carried out by individual pairs, but sometimes pairs synchronise in nest building activities. In such situations the birds all fly to the same source of mud or grass and the activity takes on the appearance of a continuous stream of birds flying to and from the source and the colony. It is relatively easy to identify the area of the colony involved in such flights, and although extremely variable, has a mean radius of ten yards.

Examination of these behavioural reactions and the infectious nature of the greeting ceremony indicates that the colony never functions as a whole, but may be considered as a series of subunits which interlink and interreact with neighbouring units. The size of these units probably changes with the season and the behavioural response involved (Figure 16).

Figure 16 Model of a kittiwake colony. The chain mail links become progressively smaller as the breeding season approaches


DIAMETER
YDS
50
20
4
SEASON

HATCHING SUCCESS

Methods

As it was possible to see into only a small proportion of the nests at Marsden, practically all breeding data were obtained from observations of the presence and number of chicks. (An investigation into the effect of the time of breeding on clutch size was made in 1976 at a colony at Dunbar, Lothian Region. Chapter 10). Counts were made twice weekly on the number of nests with chicks in each colony. The main study areas were studied in more detail: each nest was numbered, and the number of chicks in each nest was recorded twice weekly.

Kittiwakes brooding chicks, as opposed to those incubating eggs, sit in a characteristic way, with the wings held loosely away from the body. When the chicks were young, this brooding position was used as an indication of the presence of chicks. Data obtained thus fell into the following categories:-

1) chicks believed to be present, but not seen
2) chicks seen/adults seen to feed chicks
3) the number of chicks seen

As the chicks grew and were visible on each visit, they were aged (by their size and stage of feather growth), and the number seen on each visit was recorded. A check on the date of hatching and on the number of chicks hatched was thus obtained. Nests in category one were not recorded as having chicks, unless the chicks were actually seen. In 75% of the nests in which chicks were believed to be present, chicks were seen on the next visit, and in more than half of the nests incorrectly recorded, chicks were subsequently hatched.

The effect of nesting density on the date of hatching

Investigations of the time of breeding of the kittiwake have shown that several factors have a significant effect. Older females lay earlier and lay larger eggs (Coulson 1963). Moreover, the position in the colony has a marked effect: birds breeding at high density lay earlier, and birds which have changed their mate lay later than would otherwise be predicted from their age and colony position (Coulson 1972).

The relationship between the mean nesting density and mean hatching date for the main study areas in 1974, 1975 and 1976 is shown in Figure 17 and Table 16. The situation in the three years was similar, although there were some notable differences. In all three years the mean hatching date was later in the low density colonies, and earliest in the high density colony. The 1974 and 1975 data were notably alike; the difference in mean hatching date between the earliest high density colony and the latest low density colony was five days in 1974 and three days in 1975. The difference between the mean hatching date in each colony in the two years was only one day, except for the high density colony, where the difference was three days. In 1976 the range in the mean hatching dates for the main study areas was thirteen days, considerably greater than in 1974 or 1975, and again the difference between the high density colony hatching date and the next mean hatching date accounted for much of the spread (nine days). In 1974 and 1975 the time and spread of colony mean hatching dates were similar; in 1976 the spread of colony mean hatching dates was greater and the overall mean hatching date later. However, the high density colony had an earlier hatching date than in the previous two years. The delay of breeding, causing an overall late mean hatching date, was due to late breeding in the other four main study areas. The reason for late breeding in 1976 can be interpreted as resulting from unfavourable environmental conditions, causing a stress, and the presented data suggest that in such 'difficult' years the role of social stimulation

Figure 17 The effect of colony mean nesting density (number of nests within a five feet radius) on hatching date for the five main study areas in 1974, 1975 and 1976. In all years the mean hatching date is later in the low density colonies and earliest in the high density colony. In 1976 the overall mean hatching date was later than in 1974 and 1975, the high density colony alone had an earlier hatching date.

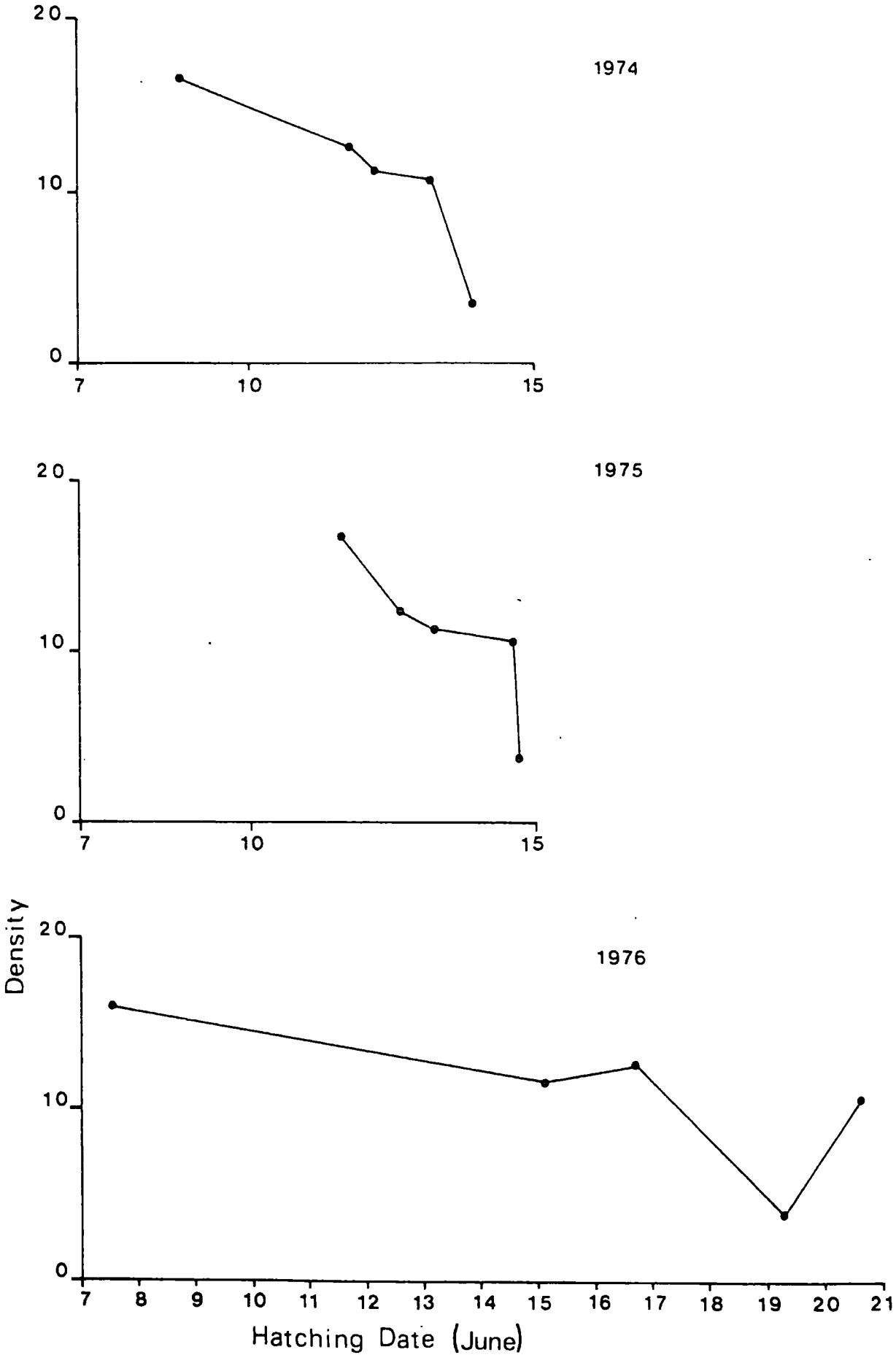

1974
1975
1976
Density
20
10
0
7
10
15
8
9
11
12
13
14
16
17
18
19
21
Hatching Date (June)

Table 16 The mean hatching dates and their standard deviations for the five main study areas in 1974, 1975 and 1976, together with the number of nests in which eggs hatched

Colony	1974	N	1975	N	1976	N
SFa	8.8 ± 4.1	90	11.6 ± 6.3	90	7.5 ± 8.8	74
NCn	11.8 ± 4.2	98	12.6 ± 5.7	108	16.7 ± 5.9	102
NCo	13.2 ± 3.5	106	14.6 ± 4.6	113	20.6 ± 8.0	110
WF	12.2 ± 5.3	181	13.2 ± 5.2	206	15.1 ± 8.0	210
SCl	13.9 ± 4.4	99	14.7 ± 5.7	111	19.3 ± 6.5	118

(the effect of nesting density) becomes more important, resulting in little or no delay among birds receiving maximum stimulation, that is, those nesting in high density areas. In the three years studied, the relationship between nesting density and hatching date is curvilinear (Figure 17). In each year, birds in the low density colony bred earlier than would be predicted by a linear relationship. From this data, and from the behavioural studies on this colony (Chapter 6, page 52), it appears that there is some compensating effect through birds in low density areas responding to others more intensively and/or over greater distances than those in high density areas.

In all years, and in 1976 in particular, the mean hatching date of the North Colony Original area (NCo) was later than would have been predicted from its mean nesting density; possible reasons for this are discussed later (page 80).

The five main study areas were broken down into 25 positional units, and again the mean hatching date was plotted against the mean nesting density (Figure 18). (Early hatching dates have low values, late hatching dates, high values.) The negative relationship is significant (1976: $r_{23} = -0.55$, $b = -0.62 \pm 0.19$, $c = +20.5$, $p < 0.01$), and predicts that for each pair nesting within a five feet radius the hatching date of any pair is advanced by 1.61 days. The effect of nesting density explains 30% of the variation in hatching date.

A similar analysis was carried out on ten areas (SF, GC, NC1, 2, 3, 4, 5, SC2, MVB, FSC) in 1975, and again the negative relationship is significant ($r_8 = -0.67$, $b = -2.05 \pm 0.71$, $c = +32.1$, $p < 0.05$) (Figure 19). However, in 1975, when the spread of breeding was less than in 1976, the relationship predicts that for each pair nesting within a five feet radius, the hatching date of any pair is advanced by only 0.49 of a day. The effect of nesting density here explains 45% of the variation in hatching date.

Figure 18 The five main study areas were broken down into 25 positional units and the mean hatching date, in 1976, of each unit plotted against the mean nesting density. The significant relationship ($r_{23} = -0.55$, $p < 0.01$), predicts that for an increase of one pair nesting within a five feet radius the hatching date of any pair could be expected to advance by 1.61 days. The effect of nesting density explains 30% of the variation in hatching date. The regression equation is

$$y = -0.62x + 20.47$$

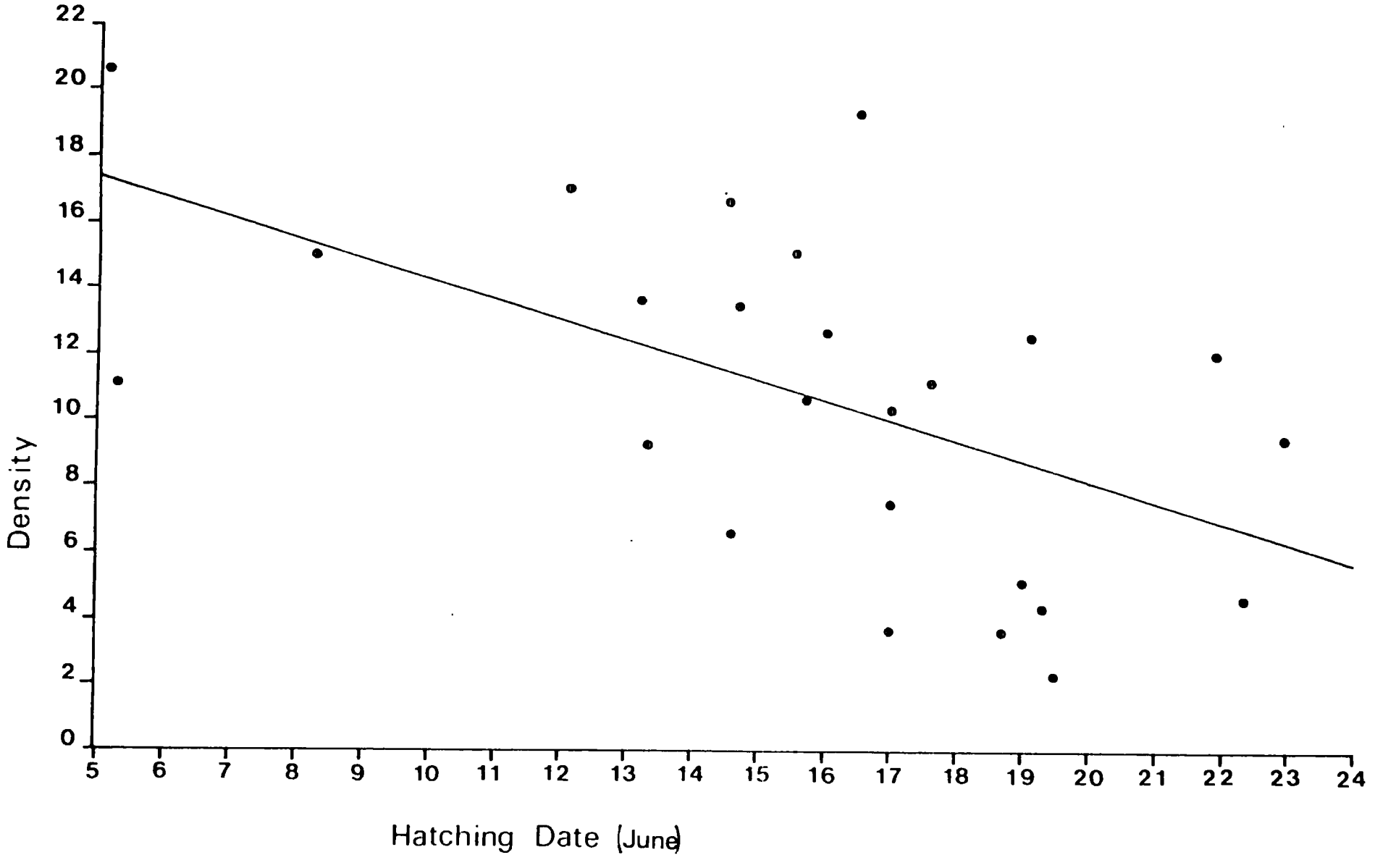
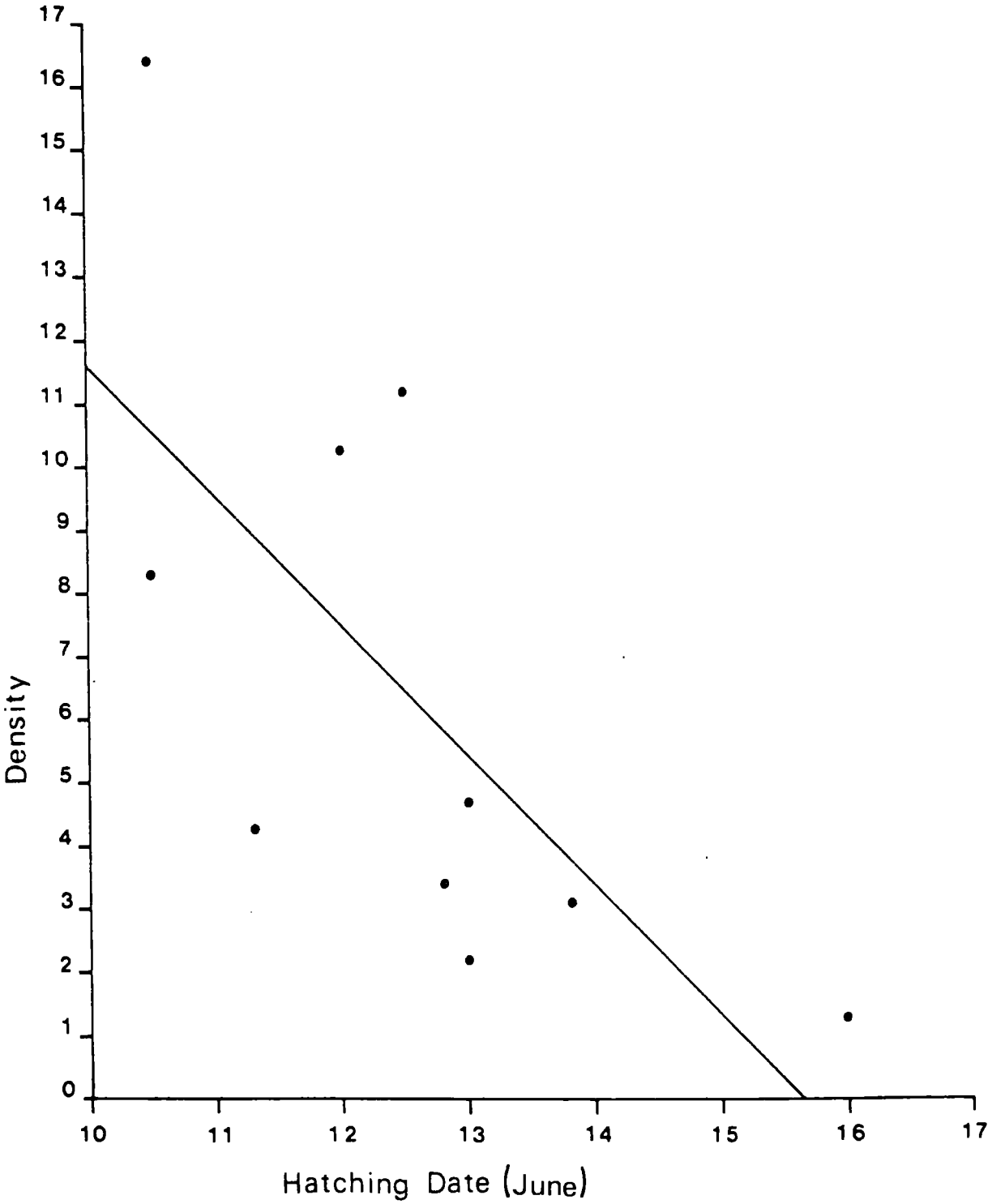

Density
0
2
4
6
8
10
12
14
16
18
20
22
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
Hatching Date (June)

Figure 19 The mean hatching dates of ten areas in 1975 were calculated and graphed against mean nesting density. Birds in high density areas bred earlier than those in low density areas. The significant relationship ($r_8 = -0.67$, $p < 0.05$) predicts that for an increase of one pair nesting within a five feet radius the hatching date of any pair could be expected to advance by 0.49 of a day. The effect of nesting density explains 45% of the variation in hatching date. The regression equation is

$$y = -2.05x + 32.1$$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Hatching Date (June)

In 1976 the effect of nesting density was greater, although it explained less of the total variation in hatching date (cf. 30% in 1976 and 45% in 1975).

Having established that colony mean density has a negative relationship with hatching date, the relationship with nesting density within a colony was investigated. The relationship between hatching date and density for 14 areas of the West Face (the largest main study area) is again negative, but is not significant ($r_{12} = -0.30$, $b = -0.53 \pm 0.45$, N.S.). The negative regression coefficient is comparable with that describing the same relationship for the 25 units of the main study areas (Figure 18). The nonsignificance of the result may in part be due to the smaller variation in mean nesting density, and partially to the small sample size.

The presented data indicate that there are differences between the colonies in the time of breeding, and much of this is explained in terms of nesting density. There are also differences in the time and spread of colony hatching dates between years.

In an attempt to quantify the effect of nesting density, the data from the five main study areas were investigated further. The density measures were broken down for each nest into the number of other nests within one, one to two, two to three, three to four, four to five, and five to ten feet, and these values were correlated, sequentially, with hatching date. A computer package programme for multivariate stepwise regression analysis was used. Tables 17 and 18 show the regression coefficients for each density value for 1975 and 1976. Although not all regression coefficients are negative in the final equation, individual values, when entered into the equation, are all negative (these values are also shown in Tables 17 and 18). The reason for this is that there are positive correlations between successive density measures. Because of the increase in nesting density as the distance from the nest increases,

Tables 17 and 18 The regression coefficients between hatching date and nesting density values for 1975 (Table 17) and 1976 (Table 18).

Because of the increase in mean nest density as the distance from the nest increases, birds at greater distance have an increased effect on hatching date, by virtue of their numbers. In addition, there is the possibility of an increased correlation between hatching date and density measures of areas further from the nest because of the greater variation in the number of nests within the area. In both 1975 and 1976 the factor to have the greatest effect on hatching date is the 5-10 feet density value, through the mean of this variable being more than six times that of the previous density value, 4-5 feet. In the final equation, after the introduction of the 5-10 feet density value, the positive and negative effects of the first five density values virtually cancel each other out. Here the 5-10 feet density value describes the relationship between hatching date and density. The relationships between hatching date and several of the preceding density variables change sign: these positive regression coefficients now describe the spread of the relationship. In both years the effect of 0-1 foot density remains negative throughout (birds at high density breed earlier), although the value of the regression coefficient is reduced through the introduction of further density values.

Table 17 Regression coefficients between hatching date and nesting density values 1975

Density Area	Mean Nesting Density	Regression Coefficient	Standard Error	p	R.C. when entered	$\bar{x}$ x final R.C.
0-1'	0.45	-0.790	0.380	<0.05	-0.932	-0.356
1-2'	2.00	+0.028	0.177	N.S.	-0.043	+0.056
2-3'	2.41	+0.124	0.164	N.S.	-0.008	+0.299
3-4'	2.77	+0.091	0.152	N.S.	-0.054	+0.252
4-5'	3.34	+0.051	0.137	N.S.	-0.083	+0.170
5-10'	22.39	-0.077	0.028	<0.01	-0.077	-1.724
					Total	-1.303

C = 15.42 R = 0.17 N = 516

Density values were introduced in order

R.C. when entered = the regression coefficient when entered into the equation: all values are negative

$\bar{x}$ x final R.C. = the product of the mean nest density and the final regression coefficient

0-1' density = the number of nests within one foot of a nest

1-2' density = the number of nests between one and two feet from a nest etc.

Table 18 Regression coefficients between hatching date and nesting density values 1976

Density Area	Mean Nesting Density	Regression Coefficient	Standard Error	p	R.C. when entered	$\bar{x}$ x final R.C.
0-1'	0.44	-0.152	0.503	N.S.	-0.969	-0.067
1-2'	0.89	-0.191	0.244	N.S.	-0.698	-0.170
2-3'	2.33	-0.027	0.232	N.S.	-0.536	-0.063
3-4'	2.65	-0.265	0.210	N.S.	-0.581	-0.702
4-5'	3.25	+0.231	0.179	N.S.	-0.050	+0.751
5-10'	21.69	-0.186	0.039	<0.001	-0.186	-4.034
					Total =	-4.285

C = 30.7 R = 0.28 N = 614

Density values were introduced in order

R.C. when entered = the regression coefficient when entered into the equation. All values are negative

$\bar{x}$ x final R.C. = the product of the mean nest density and the final regression coefficient

0-1' density = the number of nests within one foot of a nest

1-2' density = the number of nests between one and two feet from a nest etc.

birds at greater distances have an increased effect on hatching date, by virtue of their numbers. In addition, there is the possibility of an increased correlation between hatching date and density measures of areas further from the nest because of the greater variation in the number of nests within the area. In both 1975 and 1976 the factor to have the greatest effect on hatching date is the 5-10 feet density value, through the mean of this variable being more than six times that of the previous density value, 4-5 feet density.

In the final equation, after the introduction of the 5-10 feet density value, the positive and negative effects of the first five density values virtually cancel each other out. Here the 5-10 feet density value describes the relationship; the relationship between hatching date and several of the preceding density values changes sign; these positive relationships now describe the spread of the density/hatching date relationship. In both years the effect of 0-1 foot density remains negative throughout (birds at high density breed earlier), although the value of the regression coefficient is reduced from -0.932 to -0.790 in 1975, and from -0.969 to -0.152 in 1976 through the introduction of further density values.

In 1975 the variable 0-1 foot density had a significant correlation with hatching date, and in both 1975 and 1976 the 5-10 feet density value had a significant correlation. The significance of the 0-1 foot density value indicates the importance of nest position within a colony and the significance of the 5-10 feet density value, which approximates most nearly to the colony mean density, may be due to the colony itself being an important factor in determining the time of breeding. A pair may lay earlier in a low density position in a high density colony than at an equivalent density (a relatively high density position) in a low density colony.

As the age of the female is correlated with laying date, and the kittiwake shows marked nest site tenacity, there is the possibility of a close relationship between hatching dates at individual sites, in successive years. However, the correlation coefficient is only +0.17 (d.f. = 382, b = +0.12 ± 0.0060, $p < 0.001$), and although this relationship is highly significant, only 3% of the variation in hatching date is explained, and there is little risk of bias in the interpretation of data from two years from this source.

The date of return to the colony had a significant correlation with hatching date in both 1975 and 1976 (1975: $r_{514} = +0.29$, $p < 0.001$; 1976: $r_{612} = +0.33$, $p < 0.001$). Birds returning earlier bred earlier, although the effect of the date of return explained only 8% of the variation in 1975 and 10% in 1976. Having established that date of return and nesting density had an effect on hatching date, density factors and the date of return were related to hatching date 1976, using a multivariate regression analysis. The results are given in Table 19. Density values and the date of return to the colony were free to enter the equation (and were not forced in, in order, cf. Table 18). Again, 5-10 feet density is a significant factor, as is the 1-2 feet density and the date of return to the colony. As there is a positive correlation between the date of return to the colony and nesting density, the effect of nesting density is partially removed by the inclusion of the date of return to the colony. Birds in high density areas return to the colony earlier, and breed earlier. The last factor to enter the equation is the 1-2 feet density, which was selected in preference to the 0-1 foot density value because of the positive correlation between the two density variables, and the fact that the 1-2 feet density value represents a larger area, and has a greater variation in the number of nests, giving more opportunity of a higher correlation coefficient with hatching date. Together, these factors explain 14% of

Table 19 The effect of nesting density and the date of return to the colony at the start of the season on the time of breeding

Multivariate regression analysis

Dependent variable = the date of hatching 1976

Factors in the Equation	Regression Coefficient	Standard Error	p
1-2' density	-0.48	0.233	<0.05
5-10' density	-0.12	0.033	<0.001
Date of return	+0.69	0.121	<0.001

C = 31.2 R = 0.38 N = 525

Available variables not included in the equation:- 0-1' density
2-3' density
3-4' density
4-5' density

the variation in hatching date in 1976. The relationship predicts that for each pair nesting within the area of 1-2 feet from a nest, the hatching date is advanced by 0.5 of a day, and for each pair nesting within the area of 5-10 feet from a nest, the hatching date is advanced by 0.12 of a day. The importance of an earlier hatching date is in its effect on clutch size (see Chapter 10, page 100). The percentage of variation in the date of hatching, explained in terms of individual variation, is 3%, and in the latter analysis, 14%, indicating the importance of the date of return to the colony at the start of the season. The positive effects during the pre-egg laying phase are correlated with nesting density and the time spent at the colony and can be interpreted as resulting from the increased stimulation of birds in high density areas, and those present in the colony for a longer period.

The effect of nesting density on the proportion of nests in which eggs hatch

The failure of pairs to hatch eggs was investigated in 1974, 1975 and 1976 (Table 20). Although there is considerable variation in the three years, the overall mean values of the percentages of nests in which eggs failed to hatch in each colony indicate the order of success of the colonies. The North Colony New area (NCn) had a consistently low percentage of nests in which eggs failed to hatch, and the North Colony Original area (NCo) had a consistently high percentage: possible reasons for this are discussed later (page 80). To investigate the possible effect of nesting density, a multivariate regression analysis was carried out on the 1975 data; the dependent variable was 'nests in which eggs hatched, or did not hatch', (1/0), and colony and density values were independent variables (Table 21). The correlation with the 0-3 feet density variable (the sum of 0-1', 1-2', 2-3' density values) was highly

Table 20 The percentage of nests in which eggs failed to hatch in 1974, 1975 and 1976, together with the mean value for the three years for each colony, and standard errors

Colony	1974	1975	1976	Mean
SFa	30 ± 4.0	22 ± 3.9	24 ± 4.3	26 ± 2.8
WF	33 ± 2.9	23 ± 2.6	11 ± 2.0	23 ± 1.7
NCn	22 ± 3.7	17 ± 3.3	14 ± 3.2	17 ± 2.1
NCo	32 ± 3.7	28 ± 3.6	23 ± 3.5	28 ± 2.5
SCl	24 ± 3.7	26 ± 3.6	7 ± 2.3	20 ± 2.2

The North Colony New area (NCn) had a consistently low percentage of nests in which eggs failed to hatch; the North Colony Original area (NCo) had a consistently high percentage.

Table 21 The effect of colony and nesting density on hatching success.

Multivariate Regression Analysis

Dependent variable = nests in which chicks hatched/nests in which chicks did not hatch (1/0) 1975

Variables in Equation	Regression Coefficient	Standard Error	p
Colony SCl	+0.100	0.044	<0.05
Colony NCn	+0.088	0.041	<0.05
Combined 1+2+3' density	+0.024	0.005	<0.001

C = 0.62 R = 0.17 N = 814

Available variables not included in the equation:- 3-4' density, 4-5' density, colonies:- SFa, WF, NCo

significant ($p < 0.001$), high density areas having a greater proportion of nests in which eggs hatched. The positive relationship predicts that for every four pairs nesting within a three feet radius, the probability of hatching eggs in any nest is increased by 10%.

The South Colony One (SC1) was also a significant factor ($p < 0.005$); this colony had more nests in which eggs hatched than would have been predicted, as did the high density North Colony New area (NCn). However, in total, these factors explained only 3% of the variation in the number of nests in which eggs hatched. An equivalent multivariate regression analysis was performed on the 1976 data, again with 'nests in which eggs hatched, or did not hatch' (1/0), as the dependent variable. When the same variables were available, no density value had a significant correlation with the proportion of nests in which eggs hatched. The analysis was repeated, with the 0-3 feet density value forced into the equation at the first stage of the analysis (Table 22). The correlation with this density value is not significant, but describes a negative relationship; a higher proportion of nests contained chicks in the low density colonies in 1976 . (The 0-3 feet density variable described a negative relationship at all stages of the analysis.) The relationship between the proportion of nests in which eggs hatched and density in the two years is significantly different ($t_{1531} = 3.21$, $p < 0.01$). In 1976 the correlations of both the North Colony Original area and the South Face area with the proportion of nests in which eggs hatched were significant. In 1976 both these areas had proportionately fewer nests in which eggs hatched, an effect which may have been influenced by egg loss through predation.

The presented evidence indicates that the effect of density on this stage of the breeding cycle is different in different years.

Table 22 The effect of nesting density and colony on hatching success 1976

Multivariate regression analysis

Dependent variable = nests in which chicks hatched/nests in which chicks did not hatch (1/0) 1976

Variables in Equation	Regression Coefficient	Standard Error	p
Combined 1+2+3' density	-0.0022	0.0047	N.S.
NCo colony	-0.121	0.033	<0.001
SFa colony	-0.126	0.041	<0.01

N = 719 C = 0.91 R = 0.17

Available variables not included in the equation:- 3-4' density
4-5' density

colonies: WF, NCn, SCl

1+2+3 feet density was forced into the analysis at the first stage.

The 1975 data were investigated further; colony data were treated separately, and again multivariate regression analyses were used to relate the date of return to the colony and nesting density to the proportion of nests in which eggs hatched (Table 23).

In all colonies, except the high density colony (South Face Area) the immediate nesting density had a significant correlation with the proportion of nests in which eggs hatched. Eggs hatched in a higher proportion of nests in high density areas. In all colonies, except the low density colony (South Colony One), the date of return to the colony had a significant correlation, eggs being hatched in a higher proportion of nests reoccupied early in the season. Because of the effect of density on hatching date and thus, indirectly, on clutch size, it could be expected that birds in high density areas (between and within colonies) would have a larger than average clutch size, and thus an increased chance of hatching eggs. As hatching date is positively correlated with the date of return to the colony, the effect of the date of return in influencing the proportion of nests in which eggs hatch may also be mediated through the effect of hatching date on clutch size.

Table 23 The effect of nesting density and the date of return to the colony on the proportion of nests in which eggs hatched in each of the main study areas 1975

Dependent variable = whether or not eggs hatched in each nest (1/0)

Colony	Variables in Equation	Regression coefficient	Standard Error	p	N	R
SPa	Date of return	+0.165	0.080	<0.05	116	0.19
WF	1-2' density	+0.044	0.017	<0.02	267	0.30
	Date of return	+0.215	0.051	<0.001		
NCn	1-2' density	+0.053	0.023	<0.05	130	0.39
	2-3' density	+0.044	0.020	<0.05		
	Date of return	+0.220	0.083	<0.02		
NCo	1-2' density	+0.068	0.028	<0.02	156	0.26
	Date of return	+0.308	0.131	<0.02		
SCl	1-2' density	+0.131	0.040	<0.01	145	0.26

EGG PREDATION

Although adult kittiwakes at Marsden are free from mammalian and avian predation, there are several certain causes of egg and chick loss. In all kittiwake colonies a proportion of eggs fail to hatch through being infertile, and others, through being improperly incubated. Additionally at Marsden there are those eggs and chicks which are lost to predators; predation by egg collectors probably accounts for a high proportion of these eggs.

Boys were seen climbing up the cliffs, or climbing down on fixed ropes, and during the period of the present study three children were killed by falling from the cliffs, and more were injured. Because of the proximity of a cliff-top metal fence (used for rope attachment), and because of the rock formation, the North Colony Original area (NCO) probably suffered the heaviest losses, and this may in part explain the consistently high percentage of nests which failed to produce chicks in 1974, 1975 and 1976 (page 83). (Although early laying kittiwakes relay if eggs are removed shortly after laying, they do not relay if the eggs are removed late in the season (Wooller 1973).). In all three years, and in 1976 in particular, the mean hatching date of the NCo colony was later than would be predicted, and it is likely that this is due in part to higher percentages of birds relaying in this colony than in the others studied.

Rats, and rarely weasels, were seen on the beach at Marsden, and the former were seen on several occasions on the nesting ledges. Although they doubtless take a small proportion of eggs, quantifiable data were unobtainable. The South Face area (SFa) was the area of highest nesting density, and in one area kittiwakes were nesting on a steep slope which was accessible to herring gulls nesting immediately above,

on the flat top of the main stack. It seems likely, from the losses of chicks in this area, that herring gulls were responsible for chick predation, and also for egg losses in 1974, when the percentage of nests which failed to produce chicks was high, although there are no direct observations to confirm this. In 1975 and 1976 there was a successive decrease in the number of nests in the South Face area (SFa), which was mainly due to the failed nests in the upper slope area not being reoccupied.

FLEDGING SUCCESS

Differences between the colonies, and between the years

The number of chicks fledged from each nest was recorded for nests in the main study areas (Tables 24 and 25). On looking at the data for each year it is evident that there are differences between the colonies. In 1974 the South Face Area (SFa) had the lowest percentage of nests from which two chicks fledged, and had significantly fewer nests from which two and three chicks fledged than either the North Colony Original area (NCo) ($p < 0.05$), or the South Colony One (SCl) ($p < 0.05$). The poor performance of the South Face area in 1974 was due to chick predation by herring gulls (see page 80). There were no further significant differences between the colonies in 1974, and none in 1975. In 1976, however, the South Face Area had a significantly higher proportion of nests from which two and three chicks fledged than either the West Face ($p < 0.01$), or the North Colony New area ($p < 0.05$). Similarly, in 1976, the South Colony One had a significantly higher proportion of nests from which two and three chicks fledged than either the West Face ($p < 0.01$) or the North Colony New area ($p < 0.05$), and was the only colony to consistently fledge two chicks from more than half the nests (in each year, birds in the South Colony One bred earlier than would have been predicted from the colony mean density).

Colony data for the three years were summed to examine differences between the colonies (Tables 26 and 27). Because the number of nests from which three chicks fledged was small, they were grouped with those from which two chicks fledged.

Initially a Chi-square test for homogeneity was performed on the proportions of nests in which chicks hatched in the main study areas. The significant result ($\chi^2_4 = 14.7$, $p < 0.01$) shows that the situation is not

Table 24 The breeding data for the five main study areas for 1974 to 1976 inclusive

Colony	Number of Nests	Number of nests in which eggs hatched	Number of nests from which chicks fledged	Number of nests in which eggs hatched from which 0,1,2,3 chicks fledged			
				0	1	2	3
1974							
SFa	129	90	60	30	32	28	0
WF	270	181	149	32	71	78	0
NCn	125	98	92	6	33	58	1
NCo	157	106	103	3	39	62	2
SCl	131	99	92	7	33	56	3
Total	812	574	496	78	208	282	6
1975							
SFa	116	90	67	23	22	44	1
WF	267	206	178	28	50	122	6
NCn	130	108	89	19	27	57	5
NCo	156	113	87	26	37	46	4
SCl	150	111	95	16	33	60	2
Total	819	628	516	112	169	329	18
1976							
SFa	97	74	61	13	20	41	0
WF	235	210	188	22	102	84	2
NCn	118	102	87	15	43	41	3
NCo	142	110	89	21	43	44	2
SCl	127	118	100	18	35	63	2
Total	719	614	525	89	243	273	9

Table 25 The breeding data for the 5 main study areas for 1974 to 1976 inclusive

Year	Colony	No. of nests	The percentage of nests in which chicks hatched from which 0,1,2 or 3 chicks fledged				The mean number of chicks fledged/nest (successful nests only)		The mean number of chicks fledged/nest (all nests)	
			0	1	2	3	$\bar{x}$	S.E.	$\bar{x}$	S.E.
1974	SFa	129	33	36	31	0	1.47	± 0.063	0.68	± 0.071
	WF	270	18	39	43	0	1.52	± 0.042	0.84	± 0.051
	NCn	125	6	34	59	1	1.65	± 0.053	1.22	± 0.075
	NCo	157	3	37	58	2	1.64	± 0.051	1.08	± 0.070
	SCl	131	7	33	57	3	1.67	± 0.057	1.18	± 0.077
	Total	812	14	36	49	1	1.59	± 0.024	0.97	± 0.031
1975	SFa	116	26	24	49	1	1.69	± 0.059	0.97	± 0.085
	WF	267	14	24	59	3	1.75	± 0.038	1.17	± 0.056
	NCn	130	17	25	53	5	1.75	± 0.059	1.20	± 0.082
	NCo	156	23	33	41	3	1.62	± 0.062	0.90	± 0.073
	SCl	150	14	30	54	2	1.67	± 0.054	1.06	± 0.074
	Total	819	18	27	52	3	1.71	± 0.023	1.08	± 0.032
1976	SFa	97	18	27	55	0	1.67	± 0.061	1.05	± 0.090
	WF	235	10	49	40	1	1.47	± 0.038	1.17	± 0.049
	NCn	118	15	42	40	3	1.54	± 0.060	1.14	± 0.076
	NCo	142	19	39	40	2	1.54	± 0.057	0.96	± 0.073
	SCl	127	15	30	53	2	1.67	± 0.051	1.31	± 0.073
	Total	719	15	40	44	1	1.55	± 0.024	1.13	± 0.031

Table 26 Breeding data from the five main study areas, 1974 to 1976 inclusive. Colony data are summed to show up differences between the colonies.

A) shows the percentage of nests from which 0,1,2 + 3 chicks fledged. Unsuccessful nests are subdivided into those in which chicks hatched (O(H)), and those in which chicks did not hatch (O)

B) shows the percentage of nests in which chicks hatched from which 0,1,2 + 3 chicks fledged

A

	Number of young fledged			
Colony	O	O(H)	1	2 + 3
SFa	26	19	22	33
WF	23	10	29	38
NCn	17	11	28	44
NCo	28	11	26	35
SCl	20	10	25	45

B

	Number of young fledged		
Colony	O(H)	1	2 + 3
SFa	26	29	45
WF	14	37	49
NCn	13	33	54
NCo	15	36	49
SCl	12	31	57

Table 27 Breeding data for the five main study areas 1974 to 1976 inclusive. Colony data are summed to show up differences between the colonies.

A) shows the percentage of nests from which chicks fledged, and did not fledge, together with the standard error and sample size

B) shows the percentage of nests in which chicks hatched and in which chicks did not hatch, together with the standard error and sample size

A

Colony	Fledged	Did not fledge	S.E.	N
SFa	55	45	2.70	342
WF	66	34	1.70	772
NCn	72	28	2.32	373
NCo	61	39	2.29	455
SCl	70	30	2.27	408

B

Colony	Hatched	Did not hatch	S.E.	N
SFa	74	26	2.75	254
WF	77	23	1.72	597
NCn	83	17	2.14	308
NCo	72	28	2.48	329
SCl	80	20	2.21	328

uniform throughout the colonies. The colonies with the highest percentages of nests in which chicks failed to hatch (SFa and NCo) are those which suffered egg losses from predation. There is similarly a significant difference between the colonies in the proportion of nests from which chicks fledged ($\chi^2_4 = 26.5$, $p < 0.001$) although there was no significant difference in the proportions of nests from which one, or two and three chicks fledged.

Each year's data for all colonies were summed to examine differences between the years (Table 28). A Chi-square test for homogeneity in the three years on the proportion of nests from which chicks fledged indicated that there was a significant difference ($\chi^2_2 = 27.4$, $p < 0.001$). However, there were no significant differences between the years in the proportions of nests from which one chick fledged, or in the proportions of nests from which two and three chicks fledged (all nests being considered). The former effect, the significant difference between the proportion of nests from which chicks fledged, was due to the low percentage of nests in which eggs failed to hatch in 1976. In this year there was a reduction in the number of nests occupied in all the main study areas, and the low percentage of failed breeders may indicate that this reduction in sites occupied was due to the poorer or younger birds in each colony failing to breed.

From the mean number of chicks fledged per nest (Table 28) 1976 initially appears to have been a successful year, with a lower proportion of nests from which no chicks fledged than nests from which one, two and three chicks fledged ($p < 0.001$). But in 1975 there were proportionately more nests from which two and three chicks fledged (considering nests in which chicks hatched) than in either 1974 ($p < 0.01$) or 1976 ($p < 0.001$). Although the annual values for the mean number of chicks fledged from each nest indicate that 1976 was more successful than

Table 28 Breeding data for the main study areas for 1974 to 1976 inclusive. Each year's data are summed to show up differences between the years

A) shows the percentage of nests from which 0,1,2 + 3 chicks fledged. Unsuccessful nests are subdivided into those in which chicks hatched (O(H)), and those in which chicks did not hatch (O)

B) shows the percentage of nests in which chicks hatched from which 0,1,2 + 3 chicks fledged

C) shows the mean number of chicks fledged from each nest, together with the standard error

A

Year	Number of young fledged					Percentage of nests from which chicks fledged
	O	O(H)	1	2+3	N	
1974	29	10	26	35	812	61
1975	23	14	21	42	819	63
1976	15	12	34	39	719	73

B

Year	Number of young fledged				Percentage of nests in which chicks hatched from which chicks fledged
	O	1	2+3	N	
1974	14	36	50	574	86
1975	18	27	55	628	82
1976	14	40	46	614	86

C

Year	Mean ± S.E.	
1974	0.97	0.031
1975	1.08	0.032
1976	1.13	0.031

either 1974 or 1975, as there was a reduction in the number of sites occupied in 1976, this apparent success may again be due to the poorer and/or younger birds in each colony failing to breed at all. It is notable that 1976 was the year in which there was a greater spread of breeding and a late overall mean hatching date. The total number of chicks fledged from the main study areas in 1976 was less than in 1975 (1975 = 881, 1976 = 816).

Although there are some significant differences between the years, and between the colonies, no consistent pattern in the number of chicks fledged from each nest was evident.

The effect of nesting density on the proportion of nests from which chicks are fledged

To assess the effect of nesting density on the proportion of nests from which chicks fledged, the 1975 and 1976 data, relating to nests in which chicks hatched were divided into:-

a) nests from which chicks fledged

b) nests from which chicks did not fledge

Initially, a multivariate regression analysis was performed on the 1975 data in an attempt to relate nesting density, and the time of breeding, to the proportion of nests from which chicks fledged, but no single factor had a significant correlation. The analysis was repeated on the 1976 data (Table 29): both hatching date, and nesting density, had significant correlations. To compare the situation in the two years, a further multivariate regression analysis was performed on the 1975 data, but here the two factors which gave significant correlations in 1976 were forced into the analysis (Table 30). Although in 1975 neither factor had a significant correlation with the proportion of nests from which chicks fledged, the relationships are not significantly different from those in 1976.

Table 29 The effect of nesting density and the time of breeding on the proportion of nests in which chicks hatched from which chicks fledged, in 1976

Multivariate regression analysis

Dependent variable = nests from which chicks fledged, or did not fledge (1/0)

Variables in Equation	Regression Coefficient	Standard Error	p
Hatching date	-0.0011	0.0017	<0.001
3-4' density	-0.019	0.0071	<0.01

C = 1.19 N = 614 R = 0.26

Available variables not included in the analysis:- 0-1', 1-2', 2-3', 4-5', 5-10' densities

Table 30 The effect of nesting density and the time of breeding on the proportion of nests in which chicks hatched from which chicks fledged, in 1975

Multivariate regression analysis

Dependent variable = nests from which chicks fledged, or did not fledge (1/0)

Variables in Equation	Regression Coefficient	Standard Error	p
Hatching date	-0.0050	0.0026	N.S.
3-4' density	-0.0066	0.0076	N.S.

C = 0.91 N = 626 R = 0.08

The above variables were forced into the equation.

Hatching date	1975	$b = -0.0050 \pm 0.0026$
	1976	$b = -0.0011 \pm 0.0017$
3-4' density	1975	$b = -0.0066 \pm 0.0076$
	1976	$b = -0.019 \pm 0.0071$

The smaller spread in colony mean hatching dates in 1975 may have given rise to the fact that these two factors are significant in 1976, but not in 1975.

From the presented data it is evident that early breeders fledged chicks from a higher proportion of nests than late breeders, and birds in low density areas fledged chicks from a higher proportion of nests. Because of the seasonal decline in clutch size, it could be expected that, given the same hatching success, early breeders would hatch more chicks and thus improve their chance of fledging at least one chick. Having removed this effect, by the inclusion of the factor 'hatching date', nesting density exhibits a negative effect on the proportion of nests from which chicks are fledged.

From the significant relationship with density in 1976 it can be predicted that for each nest within the area of 3 to 4 feet from a nest the probability of fledging at least one chick, from a nest in which eggs hatched, is reduced by 2%.

The effect of hatching date on the number of chicks fledged from each nest

In both 1975 and 1976 the date of hatching was significantly correlated with the number of chicks fledged from each nest:

1975 $r_{626} = -0.17$, $b = -0.023 \pm 0.0055$, $p < 0.001$

1976 $r_{612} = -0.33$, $b = -0.029 \pm 0.0033$, $p < 0.001$

Early breeding birds fledged more chicks. Because of the seasonal decline

in clutch size such a relationship could be expected. The regression coefficient describing the relationship between hatching date and clutch size, obtained from the Dunbar colony for 1976, is not significantly different from the regression coefficient describing the relationship between hatching date and the number of chicks fledged in 1975, although it is significantly different from the regression coefficient describing the relationship between hatching date and the number of chicks fledged in 1976 ($t_{619} = 2.25$, $p < 0.05$).

The effect of hatching date on the number of chicks fledged in 1975 may be attributed to its effect on clutch size, although, in 1976, hatching date had an additional effect.

When only nests from which chicks fledged are considered, the relationship between hatching date in 1976 and the number of chicks fledged at Marsden is not significantly different from the relationship describing the seasonal decline in clutch size at the Dunbar colony in 1976. However, as the spread of the 'number of chicks fledged' is reduced by 25%, it is difficult to interpret this result. Hatching date may have an effect on the number of chicks fledged from each nest, in addition to its effect through influencing clutch size, although it is not marked.

The effect of nesting density on the number of chicks fledged from each nest

Using 1976 data, density values and hatching date were related to the number of chicks fledged from each nest in which chicks hatched, using a multivariate regression analysis (Table 31). Both hatching date and 5-10 feet density had significant correlations with the number of chicks fledged. Again the effect of the seasonal decline in clutch size is removed by the inclusion of the hatching date variable. Nesting density has a significant negative correlation: birds in high density areas

Table 31 The effect of hatching date and nesting density on the number of chicks fledged from each nest in which chicks hatched, for 1976

Multivariate regression analysis

Dependent variable = the number of chicks fledged from each nest in 1976 (0,1,2,3)

Variables in Equation	Regression Coefficient	Standard Error	p
Hatching date	-0.031	0.0034	< 0.001
5-10' density	-0.0073	0.0025	< 0.01

C = 2.3 N = 614 R = 0.35

Available variables not included in the equation:- 0-1', 1-2', 2-3', 3-4', 4-5' densities

fledged fewer chicks than would have been predicted from the hatching date. From the relationship it can be predicted that the number of chicks fledged from each nest is decreased by 0.007 of a chick for each pair nesting within five to ten feet of a nest. This represents a decrease of 0.6% in the overall mean number of chicks fledged from each nest, and a decrease of 13% in the number of chicks fledged from nests at the average density.

An equivalent analysis was performed on the 1975 data but, as no density value had a significant correlation, the analysis was repeated, with the 5-10 feet density value forced into the equation (Table 32). Again this density has a negative effect; the regression coefficients describing the relationship between 5-10 feet density and the number of chicks fledged from each nest in the two years are not significantly different. (1975 $b = -0.0039 \pm 0.0027$, 1976 $b = -0.0073 \pm 0.0025$). This indicates that the role of nesting density in the two years is equivalent, although in 1976 nesting density had a greater effect.

In both the analyses of factors affecting the proportion of nests from which chicks fledged, and those affecting the number of chicks fledged, nesting density was found to have a negative effect, with birds in high density areas being less successful. Although from the effects of social stimulation, and through early breeding, birds in high density areas are more successful in producing eggs, once the chicks hatch, the effect of nesting density is reversed. This is not altogether unexpected in that it could be argued that chicks in high density areas suffer both attacks from neighbouring pairs and from lack of space, particularly when the chicks are large. Although there was no evidence of death of chicks from disease or from heavy infestation of parasites in the Marsden colonies, such factors, if present, could also be expected to take a higher proportion of chicks in high density areas.

Table 32 The effect of hatching date and nesting density on the number of chicks fledged from each nest in which chicks hatched, for 1975

Multivariate regression analysis

Dependent variable = the number of chicks fledged from each nest in 1975 (0,1,2,3)

Variables in Equation	Regression Coefficient	Standard Error	p
Hatching date	-0.025	0.0055	<0.001
5-10' density	-0.0039	0.0027	N.S.

C = 1.85 N = 626 R = 0.18

5-10' density was forced into the analysis.

Available variables not included in the equation:- 0-1', 1-2', 2-3', 3-4', 4-5' densities

If a lack of space, resulting in chicks falling from the nests, was a major factor contributing to the negative effect of density on the number of chicks fledged from eggs that hatched, differences between the colonies in the ages at death of chicks could be expected. No differences were detected (Table 33). Contrary to the normal situation in a colony, nests in high density areas were those which suffered the highest losses from predation. Herring gull predation may account for the high percentage of nests in which chicks hatched, and from which no chicks fledged, in the South Face area in 1974 and 1975.

The effect of previous years' breeding success on the number of chicks fledged

As there is a positive correlation between hatching dates for individual sites in successive years, and hatching date has a negative effect on the number of chicks fledged, the possible effect of the two previous years' breeding performance on the number of chicks fledged in 1976 was examined, using a multivariate regression analysis.

Table 34 The effect of the two previous years' breeding success on the number of chicks fledged from each nest in 1976

Multivariate regression analysis

Dependent variable = the number of chicks fledged from each nest in 1976 (0, 1, 2, 3)

Variables in Equation	Regression Coefficient	Standard Error	p
Number fledged			
In 1975	+0.270	0.031	< 0.001
Number fledged			
In 1974	+0.191	0.033	< 0.001

C = 0.475 N = 819 R = 0.39

Table 33 The mean age at death of chicks in the main study areas in 1976 together with the standard deviations and sample size

Colony	Mean	S.D.	N
SFa	20.9	7.9	27
WF	23.1	9.1	87
NCn	25.4	9.4	35
NCo	24.4	9.5	42
SCl	24.1	9.0	42

Both years' breeding performance had a significant correlation with the number of chicks fledged, and together explained 15% of the variation in the number of chicks fledged from each nest in 1976. From the relationship it can be predicted that for each chick fledged in 1975 a pair will fledge 0.27 of a chick more in 1976, which represents 24% of the mean number of chicks fledged per nest in 1976. In addition, successful breeding in 1974 has an effect, in that, for each chick fledged in 1974 a pair will fledge 0.19 of a chick more in 1976, which represents 17% of the mean number of chicks fledged per nest in 1976. Birds which fledged one chick in 1974, and one chick in 1975, could be expected to fledge 0.46 of a chick more in 1976, which represents 41% of the mean number of chicks fledged per nest in 1976.

The way in which the effect of one year's breeding performance is positively related to that in the next and subsequent seasons can be explained in terms of the quality of the pair, or in terms of the quality of the nest site, i.e. through nesting density. Birds breeding in high density areas breed earlier through gaining a high level of stimulation, and through early breeding produce, on average, more eggs than those in low density areas. Because of nest site tenacity, birds which bred at high density would do so again in the following year, and again breed early. Given that egg and chick mortality is not markedly different in birds nesting at different densities, the relationship between breeding success in following breeding seasons could be mediated through nesting density. This is discussed later (page 110).

DUNBAR AND ST ABB'S HEAD

In 1976 additional kittiwake colonies were studied. At Dunbar, Lothian Region, the accessibility of two colonies made an investigation into the effect of laying date on clutch size possible. An additional Dunbar colony, and four areas at St Abb's Head, Borders Region, were studied to obtain further data on the effect of nesting density on breeding success. At Dunbar, kittiwakes nest on the old castle walls and cliffs at the mouth of a small harbour, and on the window ledges of a warehouse on the quayside. The four areas studied at St Abb's Head were cliff colonies. The three colonies studied at Dunbar were the Warehouse colony, the Castle Cliff colony and the South Cliff colony, the latter being directly opposite the Castle Cliff colony, separated from it by the harbour entrance.

It was possible, with the aid of an extendable ladder and mirror mounted on a long pole, to see into all nests in the Castle Cliff colony. From the top of the Castle Cliff colony it was possible to look down into all nests in the South Cliff colony. It was not possible to see into the Warehouse colony nests, and breeding data for this colony were obtained in the same way as for the Marsden colonies. Data for the Warehouse colony thus fell into the following categories:-

1) Site occupied by pair/single bird
2) Bird incubating eggs
3) Bird brooding chicks
4) Chicks seen/seen to be fed
5) Number of chicks seen

Both the Dunbar and St Abb's Head colonies were photographed and each nest was numbered on an enlarged photograph.

The Dunbar colonies were visited on six days during the breeding season (14 May, 26 May, 17 June, 9 July, 14 July, 3 August), and on each visit the contents of each nest were recorded; when chicks were present their ages were recorded. The Warehouse colony was observed on each visit and the data recorded as previously described.

It was possible to see into only a small proportion of the nests in the St Abb's Head colonies (A.B.C.D) and these were visited on 18 June, 14 July, 3 August. From the ages of the chicks the hatching dates were back calculated. The nesting density of each nest was described by the same method used for the Marsden colonies. Table 35 shows the mean nesting densities of each colony. Because of the availability of nest sites (window ledges) in the Warehouse colony, the majority of nests were in a line of three nests (on one ledge). They thus had a high value for 0-1 foot density, but a low overall density.

In the Castle Cliff colony 25 of the 124 clutches laid were stolen, and of the eight replacement clutches one was stolen. No eggs were recorded in ten of the occupied nests, although it is possible that in some of these nests eggs were laid and robbed between visits.

In the analysis of the effect of laying date on clutch size both replacement and stolen clutches were included if the laying date was known. The data were grouped by date into seven units of thirteen or more clutches and the mean clutch size and mean laying date for each unit calculated (Figure 20). The significant negative relationship ($r_5 = -0.92$, $b = -0.019 \pm 0.0030$, $c = +2.17$, $p < 0.01$) describes a linear decrease in clutch size as the season progresses. The overall mean clutch size of the Castle Cliff colony of 1.81 is less than that of the North Shields Warehouse colony in 1976 of 2.03. If relayed clutches are removed the mean clutch size increases, but only to 1.86 eggs/nest.

Table 35 Mean nesting densities for nests in three colonies at Dunbar, Lothian Region, and four colonies at St Abb's Head, Borders Region

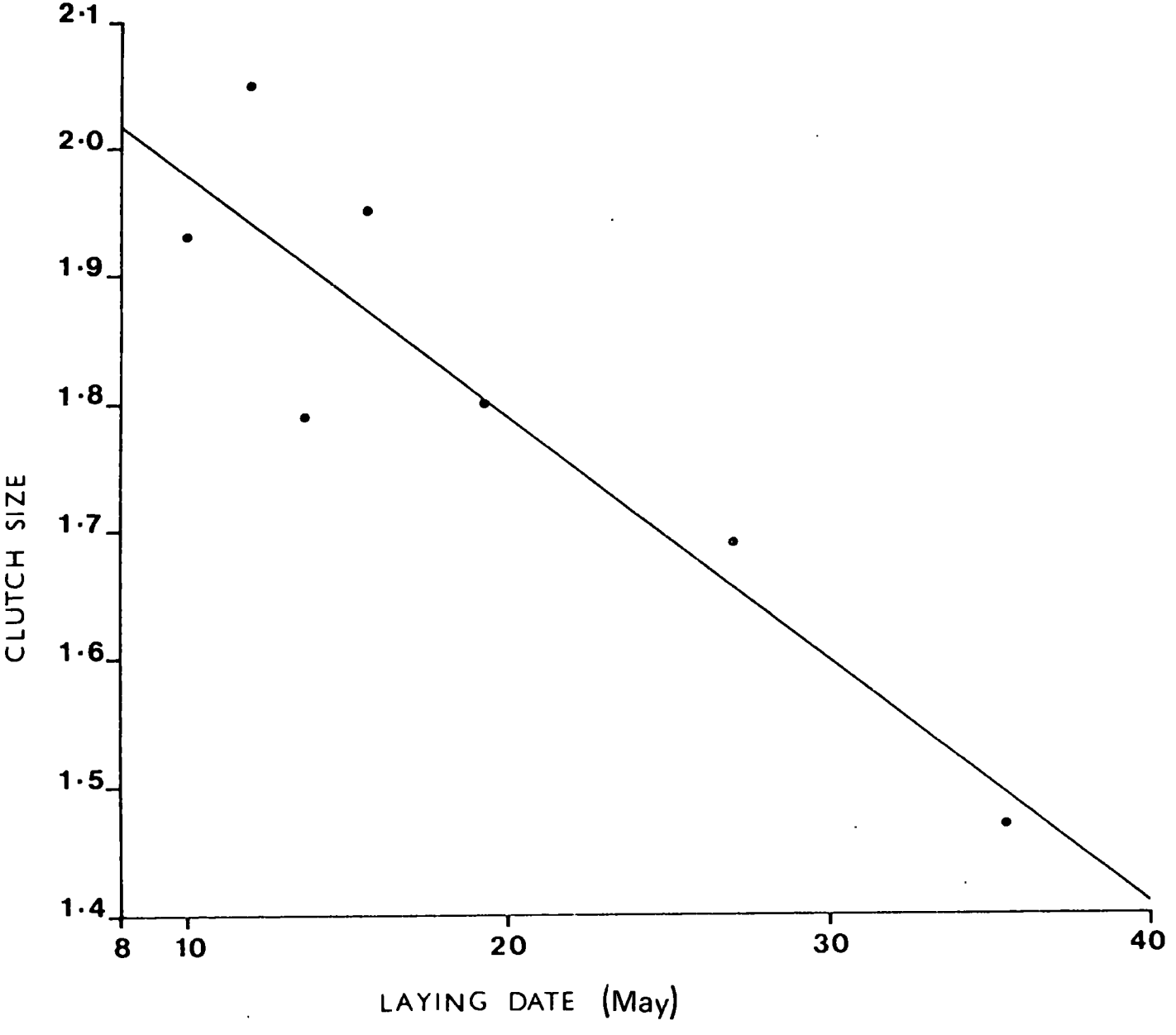
			Density					
	Colony	No. nests	0-1	1-2	2-3	3-4	4-5	5-10
DUNBAR								
	Castle	134	0.2	1.5	2.1	2.0	2.7	14.6
	South Cliff	21	0	0.3	1.0	0.9	0.4	4.7
	Warehouse	34	1.2	0.7	0.1	0	0	6.0
ST ABB'S								
	Area A	46	0.2	1.3	1.6	2.4	3.0	13.4
	Area B	29	0.1	0.5	0.5	0.6	0.7	3.7
	Area C	9	0	0.4	0	0	0	0.4
	Area D	32	1.2	1.5	1.5	2.4	3.3	19.6

0-1 density = the number of nests within one foot of a nest
1-2 density = the number of nests between one and two feet from a nest etc.

The Warehouse colony had a low overall nesting density but a high immediate density.
Area C, at St Abb's Head, had the lowest nesting density of all colonies studied.

Figure 20 Nests with eggs in the Dunbar Castle Cliff colony were grouped into units of 13 or more, and the mean clutch size of each unit was plotted against the mean laying date of each unit. The significant relationship describes a linear decrease in clutch size as the season progresses ($r_5 = -0.92$, $p < 0.001$) and is described by the regression equation,

$$y = -0.019x + 2.17$$


2·1
2·0
1·9
1·8
1·7
1·6
1·5
1·4
CLUTCH SIZE
8
10
20
30
40
LAYING DATE (May)

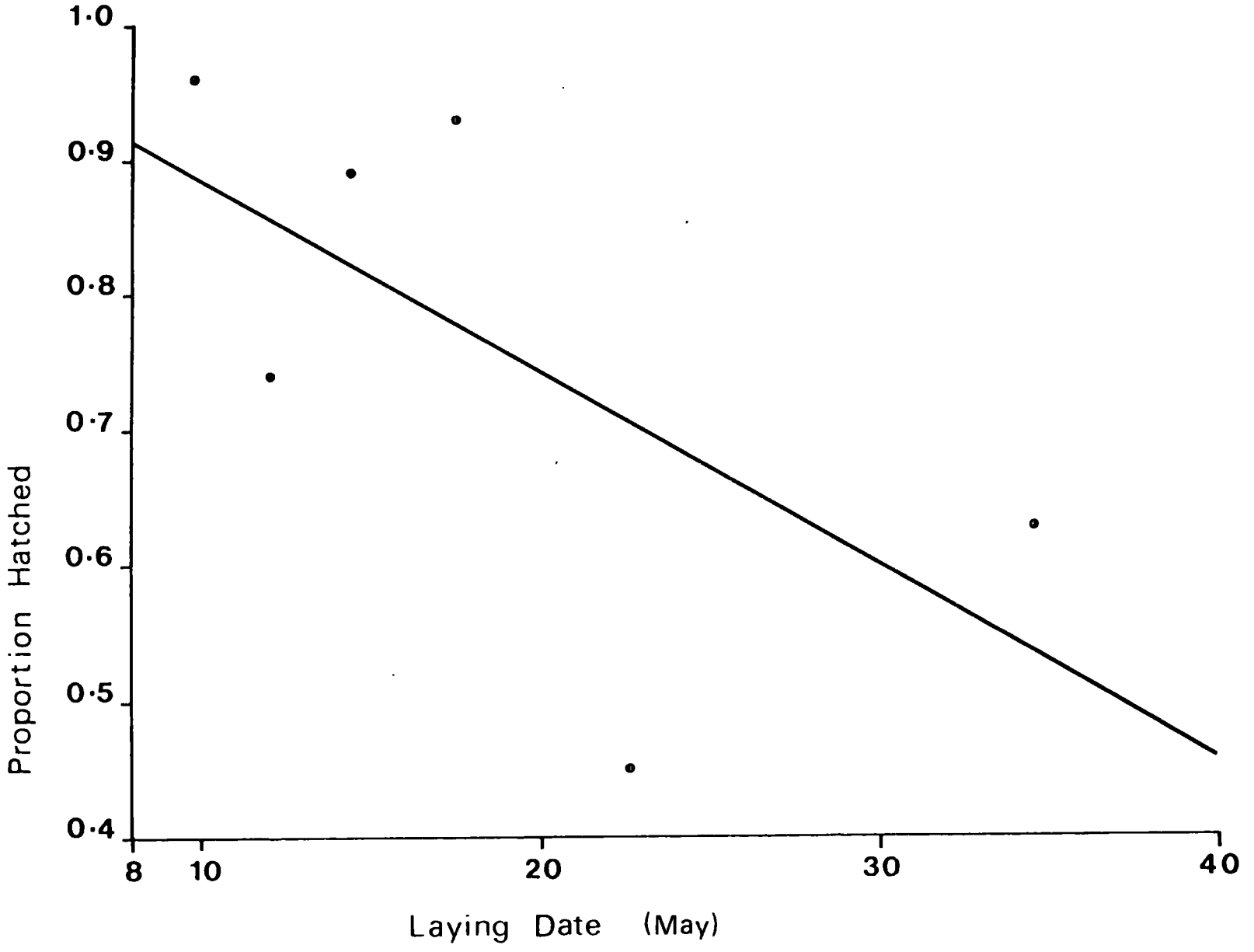
The effect of laying date on hatching failure was investigated. Nests from which the eggs were stolen were removed from the analysis, but relaid clutches were included. Again the data were grouped and the proportion of eggs that hatched was correlated with laying date (Figure 21). The correlation (r_4 =-0.63, b = -0.014 ± 0.007, c = +1.02,NS) was not significant, but the negative correlation indicates that hatching failure may be higher among the late breeders.

The South Cliff colony and Castle Cliff colony data were summed, and the relationship between the maximum number of chicks recorded in each nest and laying date investigated. The negative correlation was highly significant (r_{123} = -0.31, b = -0.026 ± 0.0071, c = +1.94, $p < 0.001$), predicting that if birds laid one day earlier they would increase the number of chicks hatched by 0.026 of a chick. Early breeders have larger clutches, and there is some indication that hatching success is greater in early breeders. These two factors give rise to more chicks being produced by early breeders.

The relationship between the number of chicks fledged from each nest and laying date was calculated (r_{123} = -0.24, b = -0.020 ± 0.0072, c = +1.60, $p < 0.01$), and predicts that by laying one day earlier, pairs increase the number of chicks fledged by 0.02 of a chick. There was no significant difference between the two regression coefficients (maximum number of chicks seen against laying date, and the number of chicks fledged against laying date), indicating that the pre-fledging mortality was not significantly higher in late breeders. In fact, the change in the regression coefficient indicates a higher pre-fledging chick mortality in early breeders. This effect may be due to the loss of one chick from three chick broods, all of which were produced by early breeders. The overall number of chicks fledged by early breeders remains higher than the number fledged by late breeders, although there is evidence that the pre-fledging chick mortality may be higher in early breeders.

Figure 21 Nests with eggs in the Dunbar Castle Cliff colony were grouped according to laying date into six units, and the mean laying date and proportion of eggs that hatched were calculated. Stolen clutches were removed from the analysis. The correlation is not significant although the negative relationship indicates that hatching failure may be higher among the late breeders ($r_4 = -0.63$, N.S.). The regression equation is

$$y = -0.014x + 1.02$$


1·0
0·9
0·8
0·7
0·6
0·5
0·4
Proportion Hatched
8
10
20
30
40
Laying Date (May)

The effect of colony and density on hatching date at the Dunbar colonies was investigated. A multivariate regression analysis was performed on the data with hatching date as the dependent variable, and colony and density values as free independent variables (Table 36). The Warehouse colony was the only factor to have a significant correlation with hatching date. The analysis was repeated, but only density values were free to enter the equation; colony values were omitted. Here, the 0-1 foot density value had a significant correlation with hatching date, and nests with a high immediate density had an earlier hatching date. Nests in the Warehouse colony have a notably high immediate nesting density. In the initial analysis the Warehouse colony explained 7% of the variation in hatching date; when it was omitted from the analysis and density values only were available, the 0-1' density value had a negative effect, and explained nearly 6% of the variation in hatching date.

The breeding success of the very low density colony at St Abb's Head is worthy of comment. Five of the nine nests had no other nests within a five feet radius, and no nest had more than one other within a radius of ten feet. Chicks were produced in only three of the nests and, in total, four chicks were fledged. The mean number of chicks fledged per nest (0.44) was less than half that of the other colonies at St Abb's Head and at Dunbar (Table 37). The most successful colony was the Warehouse colony at Dunbar (1.5 chicks fledged per nest) which had a low overall nesting density but a high immediate nesting density.

The history of the low density area at St Abb's Head is not known; the Warehouse colony at Dunbar is well established. It seems unlikely that the difference in breeding success was due to differences in age structure only. If the observed differences were due solely to age, the breeding success of the low density colony could have been expected to be higher. (The mean number of chicks fledged by first breeders at the

Table 36 1) The effect of density and colony on hatching date in the three Dunbar colonies

2) The effect of density on hatching date in the three Dunbar colonies

Multivariate regression analysis

1) Dependent variable = Hatching date 1976

Variables in Equation	Regression Coefficient	Standard Error	p
Warehouse colony	-5.94	1.54	< 0.001

C = 16.3 R = -0.27 N = 189

Available variables not included in the equation:- colonies, Castle, South Cliff, Density values 0-1', 1-2', 2-3', 3-4', 4-5', 5-10'

2) Dependent variable = Hatching date 1976

Variables in Equation	Regression Coefficient	Standard Error	p
0-1' density	-3.49	1.05	< 0.001

C = 16.4 R = -0.24 N = 189

Available variables not included in the equation:- Density values 1-2', 2-3', 3-4', 4-5', 5-10'

Table 37. The mean number of chicks fledged from each nest for the three colonies at Dunbar and the four colonies at St Abb's Head 1976

The most successful colony was the Warehouse colony at Dunbar, which had a low overall density but a high immediate density. In the least successful colony (Colony C at St Abb's head) no nest had more than one other within a radius of ten feet.

Colony	Number of nests	Mean number of chicks fledged/nest	0-5' Mean Density
DUNBAR			
Castle Cliff	134	0.95	8.5
South Cliff	21	1.24	2.6
Warehouse	34	1.50	2.0
ST ABB'S HEAD			
A	46	1.24	8.5
B	29	1.41	2.4
C	9	0.44	0.4
D	32	1.22	9.9

Warehouse colony at North Shields is 1.05 (Thomas, pers. comm.).) The most obvious difference between the colonies is in their nesting density, and in view of the effects of nesting density on hatching date and through hatching date on clutch size, it could be expected that the birds in the low density colony would have a smaller clutch size. However, this effect and the effect of density on hatching date do not explain the difference in the mean number of chicks fledged from each nest in the two colonies. It is probable that a higher proportion of pairs in the low density areas received insufficient stimulation to lay eggs, although the nine pairs in the low density area built nests. It could be expected that, because pairs cannot breed in isolation, some females in very low density areas would receive insufficient stimulation, from the mate and from the few surrounding pairs, to produce eggs.

The poor performance of this very low density St Abb's Head colony upholds these expectations. In contrast, birds in the Dunbar Warehouse colony, with a high immediate nesting density, had a high breeding success. Birds received a high level of stimulation from the relatively large number of other pairs in close proximity, bred earlier, and through early breeding would have had a larger clutch size, resulting in this colony fledging, on average, more chicks than birds in the lower density areas, and those with a lower immediate nesting density, but a higher value for 0-5 feet density.

DISCUSSION

Typically, populations show phenomena associated with density. A peculiar characteristic of certain biotic factors such as predation, competition, parasites and pathogens is that they exert an adverse effect on numbers that is positively related to density. For all populations there is an upper size limit, with the action of density dependent factors reducing the rate of population growth before this level is reached (Nicholson and Bailey 1935, Andrewartha and Birch 1954, Krebs 1972). The role of density dependent factors is of considerable importance in population regulation: accordingly it has been the subject of much research (examples are given in Allee *et al.* (1949) and Krebs (1972)). At high density most animals are less successful: reproductive success or longevity is reduced, and both effects may occur together. Reduced longevity and fecundity are typical of high density populations of certain mammals (Southwick 1958, Christian 1956, Conaway, Baskett and Toll 1960, Taber and Dasmann 1957) and many other animals (Ullyett 1950, Smith 1963). There is evidence that increased density similarly causes a decrease in the clutch size in some birds (Lack 1952, 1966; Perrins 1965), although the effects of deferred maturity and increased adult mortality rate may be more important in the regulation of population size (Lack 1954). In addition, birds in high density areas may be prevented from breeding by the interference from surrounding pairs. Productivity is reduced in dense breeding colonies of Canada geese due to a failure of the birds to pair successfully, or to lay and incubate eggs (Collias and Jahn 1959), and neighbouring birds interfere with nest building in the zebra finch (Bruen and Dunham 1973).

It is important to distinguish the concept of overcrowding from that of crowding in social animals. Overcrowding is used to describe a population where the negative effects of density are deleterious to the

population as a whole. In colonial animals, which crowd together rather than distributing themselves more evenly, the adverse action of density dependent factors on populations becomes important only at considerably higher densities than in non-colonial species. It must therefore be assumed that such colonial species derive overall benefit from this form of behaviour.

Possible advantages in colonial breeding in birds could arise through social stimulation resulting in more synchronised breeding and a 'swamping' of predators (Darling 1938), population regulation (Wynne-Edwards 1962), information centres for food finding (Ward and Zahavi 1973), or through reduced predation through detecting predators earlier and/or deterring them more efficiently (Sears 1979, Birkhead 1977). The advantage in synchronous breeding resulting in reduced predation or benefits from social foraging has been demonstrated (Patterson 1965, Horn 1968, Emlen and Demong 1975, Parsons 1976, Hoogland and Sherman 1976).

Because the scope of possible advantages in coloniality is diverse, in the present study the search for such advantages was restricted to investigating the role of nesting density. Although it is possible that social breeding in the kittiwake arose from advantages in more synchronised and coordinated breeding resulting from social stimulation, it is more likely that coloniality arose out of an existing breeding system, possibly through advantages derived from reduced predation and the limited availability of cliff face nest sites (Cullen 1957). Certainly in most colonial species the action of mammalian predation is minimised by their choice of inaccessible nest sites, such as islands, tree tops and cliff faces.

In general, animals breed only during a particular season of the year. Such a degree of synchrony has a selective advantage in that the timing of the breeding season can be a direct adaptation to the most efficient utilisation of some ecological factor, e.g. the production of

young at a time when food is most readily available. It has been shown that, in many vertebrate species including birds, changes in light stimuli due to changing day length constitute one of the principal triggers for gonad development (Marshall 1942, Bullough 1951). Synchrony in breeding similarly occurs in invertebrate groups (Danilevskii 1965, Cloudsley-Thompson 1961), the most widely quoted example being the marine polychaetes, the palolo worms (Eunicidae) where reproduction is highly synchronised by the lunar cycle (Clark 1941).

Although increasing day length in spring gives rise to gonad development in many birds, stimulation from the mate is required before the attainment of full reproductive condition in many species (Eisner 1960, Lehrman 1959, Lehrman and Friedman 1969).

In the kittiwake the presence of other breeding individuals is essential for successful breeding, resulting in coloniality, and the mutual stimulation of members of the colony. Thus, although the environmental trigger for gonad development is the same in each bird, as the rate of gonad development is accelerated by neighbouring birds, the actual timing and synchrony of breeding within colonies is variable. A similar situation is seen in the equatorial swallow-tailed gull (Hailman 1964) and the herring gull (Parsons 1976) where local synchrony is seen in groups within the colony.

In the present study, nesting density was found to affect several stages in the breeding cycle (Table 38). The effect of nesting density caused differences both within and between colonies. The effect of density was not found to be one relating to overall colony density as the Darling hypothesis proposes (Darling 1938); immediate nesting density is more important than the mere acquisition of a nest site within that colony, in that birds in close proximity had a greater effect than those further away.

Table 38 The effect of nesting density on stages in the breeding cycle

STAGE	THE EFFECT	THE MAGNITUDE OF THE EFFECT
1. The return to the colony at the start of the season	Birds that nested at high density in the previous year return earlier	The date of return to the colony at the start of the next season is advanced by 2.5 days for each pair nesting within 5 feet of a nest
2. The date of laying	Birds in high density areas tend to breed earlier	In 1976 the hatching date was advanced by 1.6 days, and in 1975 by 0.49 of a day for each pair nesting within 5 feet
3. Clutch size	There is a seasonal decline in clutch size. Density has an indirect effect through laying date	By laying one day earlier the clutch size is increased by 0.019 of an egg
4. The proportion of nests in which chicks hatch	The effect of nesting density is not consistent	In 1975 the chance of hatching at least one egg was increased by 2.4% for each pair nesting within 3 feet of a nest. In 1976 the effect was reversed (-0.22%) but was not significant
5. The proportion of nests in which chicks hatch from which chicks fledge	Birds in high density areas fledged fewer chicks and from a lower proportion of nests than would be predicted from the laying date	In 1976 the probability of fledging at least one chick from a nest in which eggs hatched was reduced by 2% for each pair nesting within 3-4 feet of a nest

Continued overleaf.....

Table 38 (continued)

STAGE	THE EFFECT	THE MAGNITUDE OF THE EFFECT
6. The number of chicks fledged from nests in which chicks hatch		The number of chicks fledged from each nest in 1976 was reduced by 0.007 of a chick for each pair nesting within 5-10 feet. In 1975 both relationships were equivalent although the correlations were not significant (i.e. stages 5 and 6).
7. The departure from the colony at the end of the season	Birds in high density colonies tend to vacate the colony later	
8. The return to the colony	Birds that nested at high density return earlier at the start of the next season	As 1.

At the onset of a new breeding season, birds which bred at high density in the previous year returned earlier, and those birds that left the colony later in the previous season returned earlier. The effects of one breeding season are carried forward to the next.

Differences in the date of return to the colonies are doubtless governed by a complexity of factors, not only those influencing the hormonal state of the bird (including social stimulation from the previous year), but also those factors of the physical environment which affect the general condition of the bird. Thus Uspenski (1958) reported that kittiwakes in Novaya Zemlya return to the colony in mid April, but in some years are prevented from occupying the breeding ledges because they are still covered with snow. The nests are occupied as soon as they are free from snow, and nest building commences soon afterwards. The dates of return to high latitude colonies are shown in Table 39. Accepting that the date of return to the colonies is ultimately under the influence of endocrine secretion, changes in the physical environment exert a regulating influence which brings the behaviour into line with those changes.

The data on the proportions of birds in breeding plumage at the start of the season are indicative of the fact that there are hormonal differences related to the breeding condition of the bird at the time of return to the colony. Birds nesting at high density, which return earlier, are on average already more advanced in terms of breeding condition. There is no evidence to suggest segregation within the wintering feeding areas of birds which nested at different densities, nor is there evidence that the colony group is maintained during this period; certainly it is difficult to envisage the birds retaining their spatial relationships. If birds from high and low density areas disperse and winter in similar areas, then the difference found in the proportions of birds in breeding plumage in the different colonies can not be mediated through increasing day length

Table 39 The time of return to the colony, the date of laying of the first egg, and the mean clutch size for kittiwake colonies at different latitudes

Authority	Date of return	Date of 1st egg	Mean clutch	Years studied	Colony
Coulson (pers.comm.)	January	1st week in May	2.07	1954-78	North Shields, Tyne and Wear
Belopol'skii (1961)	March	$\bar{x}$ = 17/5 Mid May	1.96	1937-40	East Murman
Uspenski (1958)	Mid April	10/6, 11/6, 11/6	?	1948-50	Novaya Zemlya
Swartz (1966)	Late May	21 - 25/6	1.84	1960-61	Alaska

nor stimulation when away from the colony. Again the data indicate that the effect of nesting density in one season is carried forward to the next. Because of mate and nest site tenacity, the argument that has been applied to other species that birds at a similar stage in their reproductive cycle pair and breed, giving synchrony, is not applicable to the kittiwake. It is not envisaged that kittiwakes receive stimulation when away from the colony, in contrast to what may happen in the tricoloured blackbird (Orians 1961) where nomadic birds may receive stimulation in the very close knit flocks prior to breeding, or the sandwich tern where breeding birds ready to lay enter the colony and nest together (Langham 1974).

A study of the infectious nature of the greeting ceremony in the kittiwake is perhaps the most obvious way of measuring the effect of one pair on another, and of obtaining a measure of the amount of stimulation received by a pair from surrounding pairs. Birds receive the strongest stimulation from those which are in close proximity but, because there are more nests at increasing distances from a nest, a higher proportion of stimulation is provided by those nesting a short distance away. Examination of these behavioural reactions (and those of nest building and of panic flights) leaves a clear impression that the colony never functions as a whole, but as a series of subunits which interlink. Although nesting density is exerting an effect, it is not one of colony mean density, although such a generalised measure will show up differences between high and low density colonies. Birds nesting at low densities, as opposed to those nesting at high densities, respond more readily to birds at greater distances from them, and this can be interpreted as a compensating effect. Pairs in low density areas not only receive less stimulation from their neighbours by virtue of having fewer of them, but are present in the colony for a shorter period, returning later at the start of the season and leaving

earlier at the end of the season. Birds in high density areas respond as readily as birds in low density areas to those which are immediately adjacent; they respond less readily to those at greater distances. As an increase in stimulation enhances breeding success, the compensating effect seen in the low density colony is clearly of value.

When a pair performs the greeting ceremony, although the effect is passed to neighbouring pairs, which themselves then perform the greeting ceremony, the effect is not passed throughout the colony, or rarely so. It is possible that the sight of a bird landing on an adjacent site, coupled with the performance of the greeting ceremony, provides an increase in the stimulation of surrounding pairs; such pairs appear to perform a less intense greeting ceremony and of shorter duration than re-united pairs.

For several species it has been reported that the performance of courtship or nest building behaviour by one pair, or groups of pairs, can stimulate others to do the same, resulting in a synchronisation of activities (Southern 1974, Emlen and Miller 1969, Brown 1967, Collias, Victoria and Shallenburger 1971, Darling 1938), and the positive effect of social stimulation in enhancing pair formation has been shown (Hall 1970). Erickson and Lehrman (1964) showed that ovarian activity in female ring doves was a direct reflection of the vigour of male courtship activity, and Erickson (1970) suggested that the frequency of a particular component of the male display (nest soliciting) was particularly significant in influencing the female ovarian response, as measured by the development of the reproductive tract.

There is evidence to suggest that, in the kittiwake, the stimulatory effects of nest density will be found to depend upon inter-individual (between mates and between neighbouring pairs) stimulating effects on the endocrine system; the female being only physiologically

ready for copulation after a period of courtship by the male, of stimulation from him, and from surrounding pairs. One selective advantage in such a system is that it allows time for the establishment of a durable pair bond, a necessity for successful chick rearing. Kittiwakes which return to the colony early tend to breed earlier. Although older females lay earlier, the effect is not only one of age, but is closely related to nesting density. Birds nesting at higher density lay earlier, and because of the seasonal decline in clutch size have, on average, larger clutches. Thus within any year, density exerts its effect on the possible breeding potential of pairs by influencing the number of eggs laid.

In view of the fact that pairs of kittiwakes are unable to breed in isolation, the factors stimulating pairs to breed must be from colony neighbours, in addition to those from the mate. It seems plausible that the same mechanism that controls whether or not kittiwakes breed exerts its influence on the time of breeding and possibly also on clutch size.

Very few first breeding females lay three egg clutches: in older females, and only amongst those which have a relatively early laying date, are three egg clutches common. The pre-egg laying period may be envisaged as a 'stimulation period', the optimum strategy being to gain enough stimulation to breed early and through early breeding to produce a three egg clutch. All birds, except the late breeders, have the potential to lay more than two eggs, and this is evident in the fact that such birds will relay if clutches are removed shortly after laying (Wooller 1973). It is therefore relevant to consider why early breeders lay a higher proportion of two and three egg clutches, and why there is a seasonal decline in clutch size. Because of the positive correlation for individual sites in successive years, the increased breeding success through early laying and producing a larger clutch is not restricted to any one

year, but is seen in subsequent breeding seasons. An equivalent situation is seen in the Adélie penguin where there are consistent differences in the clutch size of individual females related to the date of laying (Spurr 1975).

In years when breeding is late, a lower proportion of three egg clutches could be expected, and this has been shown by Belopol'skii (1961) in northern Russia where the breeding season varies considerably from year to year. At Marsden it was not possible to record the clutch size, breeding data being obtained from the numbers and ages of chicks. As factors such as overcrowding, causing the loss of one chick from a three chick brood, could be expected to be different in the different colonies, the search for such differences introduces a strong bias. However, differences between the years in the proportions of three chick broods could be expected. It is notable that in 1976, when breeding was later, three chicks were fledged from fewer nests than in 1975 (cf. 18:9).

An alternative theory to explain the production of three rather than one or two eggs per clutch lies in the behaviour of birds during egg laying. There is evidence for several species to show that both tactile and temperature stimulation of the brood patch by the eggs suppresses the secretion of FSH from the pituitary (Bailey 1952). This in turn causes an increase in prolactin secretion, which gives rise to the degeneration of further developing follicles. Subsequent eggs are prevented from developing and the clutch is complete. It may be that those birds which lay three eggs start incubation at a slightly later stage and thus do not suppress the production of a third egg. In early breeders, few of the surrounding pairs would be incubating at this time, but would still be involved in both courtship and nest building, both activities which stimulate the secretion of FSH from the pituitary.

In the Marsden colonies the effect of nesting density on the proportion of nests in which eggs hatched was positive in 1975 but negative in 1976. It could be expected that high density areas, where breeding is earlier, would have a higher proportion of nests in which eggs hatched. The cause of the negative action of density in 1976 has not been isolated, although it could be explained in terms of the presence of a density dependent factor, such as a pathogen, which would account for a higher proportion of addled eggs in high density areas through increased transmission.

After the removal of the effect of the date of hatching, birds in high density areas fledged fewer chicks than those in low density areas, and from a lower proportion of nests in which chicks hatched. Although the factors causing this have not been identified, disadvantages to chicks in high density areas could arise through physical interference from surrounding pairs, competition for space, brood parasitism and/or the increased transmission of parasites and disease (although there was no evidence of chick mortality through disease or parasitism at Marsden), and in these colonies, predation.

It is evident that the effect of nesting density is not positive throughout the breeding season. However, for kittiwakes to remain intensely colonial, the advantages in nesting density (e.g. through increased social stimulation) must outweigh the disadvantages (e.g. the increase in agonistic encounters and the greater time and effort required to retain the nest site). Although the advantages in increased protection from predators and from social foraging have been shown for other species, there is no evidence to suggest that the kittiwake derives such benefits from colonial breeding.

Throughout the study it was evident that there are differences between the birds in the high and low density colonies, and that the effect of nesting density is not restricted to that year, but is carried over to the following year. There is evidence to show that there are differences in the quality of male recruits at the time of recruitment (Wooller and Coulson 1977), although there is, at present, no evidence to show that such differences have a genetic basis. Differences in the quality of recruits to the high and low density areas could be enhanced by an increased feeding efficiency of the heavier recruits to high density sites. Whatever the basis of such differences, the effects are far reaching, in that the reproductive performance of birds in high density areas is not only higher in any one year, but is consistently higher throughout the life of the bird. (At the North Shields colony male birds in high density areas produced, on average, 88% more chicks than males in low density areas throughout their life-time (Coulson and Dixon 1979).)

The fact that birds which change their mate due to the death of their former partner do less well than those which retain the same mate from the previous year (Coulson 1966) again indicates the importance of pairing early in the season, and the importance of stimulation. If differences between such pairs were due to the quality of the birds, and not the time spent together prior to breeding, such differences would be less marked, if present at all, in that it could be expected that in half of the cases the new mate would be of higher quality than the previous mate. As there is a tendency for birds to mate with a bird of similar breeding experience (Coulson 1966), these differences are not explicable in terms of age (e.g. the new mate being a first breeder). In addition, the effect of the change of mate is carried forward to their second year of breeding together, in that birds which retained their mate for three years are more successful than those which bred together for two years.

An equivalent situation exists in the ring dove, where familiar pairs are more successful in hatching eggs (Erickson and Morris 1972).

After the chicks have fledged there is a resurgence of courtship activity and pairs spend longer together. Uspenski (1958) reported nest building activities during this period, although the nests were never completed. It could be expected that birds in high density areas would again receive more stimulation from surrounding pairs, leading to an increased secretion of FSH, and through this, increased growth of gonads. The higher levels of reproductive hormones in these birds could account for the delayed departure from the colony. In association with this, gonad regression in birds that nested in high density areas would be less extreme when the annual redevelopment of the gonads begins, triggered by an increasing day length. Those birds from high density areas would already be at a more advanced stage, resulting in an earlier return to the colony, and an earlier prenuptial moult.

Once present in the colony, early pairing and the increased stimulation from the higher numbers of neighbours in close proximity would result (through a direct influence on hormone secretion) in earlier maturation of the gonads, and thus an earlier date of laying. Birds in high latitude colonies necessarily leave the colony early because of the adverse climatic conditions, and thus have a longer period for gonad regression before the annual gonad redevelopment is triggered, resulting in a longer redevelopment phase, and a later arrival at the colony at the start of the next season.

During the pre-egg laying phase, birds which paired late due to the death or divorce of their former mate would have a shorter stimulation period, as would those birds that arrived back late at the start of the season. Accepting that there are differences in the quality of the birds at the time of recruitment, differences between birds nesting in areas of high and low density could be strongly influenced by the quality of the nest site, that is, nesting density and the effect of social stimulation.

There is evidence that stimuli from the mate, from activities of surrounding birds, from the nest or eggs, and from the young can actually stimulate changes in hormone secretion in birds (Lehrmann 1959), and thus influence the succession of changes in physiological state. There is thus a reciprocal arrangement, changing hormone patterns influencing behaviour, and changing environmental conditions, including behaviour, influencing hormone secretion.

It would be advantageous for further studies of the effect of social stimulation to concentrate on those species where all group behaviour can be monitored, and where birds of known age and breeding experience can be studied. Before the effect of social stimulation in the kittiwake can be fully understood, a detailed knowledge of the changing patterns of hormone secretion is required. It is hoped that students of bird behaviour can give added stimulation to those of avian physiology.

SUMMARY

1. The effect of nesting density on the time of breeding and on breeding success was studied from 1974 to 1976 inclusive, at the kittiwake colonies at Marsden Bay, Tyne and Wear: five areas were chosen for detailed study. In 1976, observations were extended to other colonies in Northeast England and Southeast Scotland.

2. The nesting density of all nests in the five chosen areas was measured by recording the number of other nests within 1, 1-2, 2-3, 3-4, 4-5, 5-10 feet of each nest. For all other colonies a colony mean density measure was obtained by using the boundary strip method.

3. The order of return to the colonies at the start of the season follows the order of colony mean density. The relationship predicts that a bird will return 2.5 days earlier at the start of the following season for each additional pair nesting within a five feet radius. Within colony differences not related to nesting density were attributed to differences in the age structure of different areas.

4. There is a negative relationship between the date of departure from the colony at the end of the season and the date of return to the colony at the start of the following season. The relationship predicts that a bird will return 4 days earlier at the start of the next season for each additional day that it remains at the colony at the end of the season. There is a positive correlation between the dates of arrival to the colony for individual nest sites in successive years ($r_{817} = +0.44$).

5. During the reoccupation phase, wind speeds of above eleven knots caused a decrease in the number of sites occupied, and the number of pairs present.

6. On individual days during the reoccupation phase, the percentage of birds in breeding plumage in each colony is positively correlated with nesting density. On days when the number of birds present in the colonies was

below the expected level, the proportion of birds in breeding plumage was above the expected level.

7. The infectious nature of the greeting ceremony was investigated during the pre-egg laying period. The distance over which pairs respond is usually restricted to a radius of five feet from the reunited pair. Birds in low density areas respond more readily to greeting ceremonies which take place at greater distances from them. It was evident from observations of the three activities in which there are clear responses in neighbouring individuals (panic flights, nestbuilding, the greeting ceremony) that the colony never functions as a whole, but as a series of interacting and interlinking sub-units.

8. Data obtained from a colony at Dunbar, Lothian Region, show that there is a linear decrease in clutch size as the season progresses. The relationship predicts that by laying 10 days earlier, the clutch size is increased by 0.19 of an egg. The number of chicks fledged from each nest is positively correlated with laying date: by laying one day earlier the number of chicks fledged from each nest increased by 0.02 of a chick. Nests with a high immediate nesting density are more successful than those with a low immediate nesting density but a higher overall 0-5 feet density. The differences in breeding success between the colonies (ranging from 1.50 chicks fledged per nest, to 0.44 chicks fledged per nest) are not explicable in terms of possible differences in the age structure in the colonies.

9. The spread and timing of colony mean hatching dates in the Marsden colonies were different in different years. In 1976 the spread of colony mean hatching dates was greater than in either 1974 or 1975. Birds breeding in high density colonies were consistently early, and in low density colonies consistently late, although birds in the colony with the lowest mean nesting density bred earlier than would have been predicted from a linear relationship between hatching date and nesting density. The relationship between hatching date and density in 1975 predicted

that birds would lay 0.49 days earlier for each pair nesting within a five feet radius. The equivalent relationship in 1976, when there was a greater spread of breeding, predicted that birds would lay 1.61 days earlier for each additional pair nesting within a five feet radius. A multivariate regression analysis, performed on the 1976 data, related individual nesting density values to the time of breeding and predicted that the hatching date of any pair would be advanced by 0.5 of a day for each additional pair nesting within the area of 1-2 feet from a nest, plus 0.12 of a day for each additional nest within the area of 5-10 feet from a nest.

10. The proportion of nests in which chicks hatched was positively correlated with nesting density in 1975. For each pair nesting within three feet of a nest, the chance of eggs hatching in that nest was increased by 2.4%. The correlation between the proportion of nests in which eggs hatched in 1976 and nesting density was not significant, but described a negative relationship.

11. Hatching date is positively correlated with the proportion of nests from which chicks fledged, due to the effect of the time of breeding on clutch size. Having removed this effect, nesting density has a negative effect on the proportion of nests from which chicks are fledged. In 1976 the probability of fledging at least one chick from a nest was reduced by 2% by each pair nesting within the area of 3-4 feet from a nest. The correlation in 1975 was not significant, but the relationship was equivalent.

12. Nesting density has a negative effect on the number of chicks fledged from each nest. In 1976 the significant relationship described a reduction in the number of chicks fledged of 0.007 of a chick for each pair nesting within the area of 5-10 feet from a nest. This represents a decrease of 13% of the mean number of chicks fledged per nest for nests

at the average nesting density. The relationship for 1975 was equivalent but not significant.

13. The number of chicks fledged from each nest is positively correlated with breeding success in the two previous years. Birds which fledged one chick in 1975 fledged 0.27 of a chick more in 1976, and those which fledged one chick in 1974 fledged 0.19 of a chick more. Successful breeding in 1974 and 1975 (fledging one chick in each year) resulted in fledging 0.46 of a chick more in 1976, which represents 41% of the mean number of chicks fledged per nest in 1976.

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APPENDICES

The number of other nests within a five feet radius, for each of the main study areas, 1975

No. of other nests within 5' radius	WF	NCn	NCo	SFa	SCl
0	2	1			8
1	1		1		16
2	5		2		31
3	11	5	3		17
4	6	7	4	1	18
5	4	6	3	2	28
6	7	4	10	1	11
7	17	8	9	4	11
8	20	11	9		9
9	26	6	13	2	1
10	31	14	12	3	
11	25	2	17	4	
12	16	3	23	3	
13	18	5	12	7	
14	15	8	17	11	
15	11	7	8	4	
16	12	6	7	11	
17	13	5	1	12	
18	7	11	2	8	
19	6	2	2	6	
20	5	4		7	
21	5	1		11	
22	2	6	1	6	
23	1	4		1	
24		1		4	
25	1	2		5	
26				3	
27		1			

The percentage of sites occupied in eight colonies, during the reoccupation phase, 1975

	Percentage of sites occupied							
Date	SF	MVB	WF	FSC	NC	SC2	SC1	GC
6.1	0.5	0	0	0	0	0	0	0
7.1	17	0	24	0	2	0	0	2
9.1	16	0	15	0	4	0	0	4
10.1	35	0	27	2	17	1	1	2
14.1	4	0	3	0	0.5	0	0	0.3
16.1	28	-	26	-	2	-	-	-
17.1	43	1	27	3	23	0	1	9
20.1	46	0	29	7	28	6	0	27
23.1	29	0	14	0	5	1	1	11
27.1	59	33	41	24	43	13	13	84
30.1	60	42	40	47	56	34	29	71
3.2	66	50	49	49	53	52	51	67
10.2	67	62	54	65	64	50	64	70
17.2	70	43	49	56	69	71	64	74
24.2	74	78	63	72	67	64	78	87

The percentage of sites occupied in the main study areas, during the reoccupation period, 1976

	Percentage sites occupied				
Date	SF	NCn	WF	NCo	SCl
5.1	19	9	9	5	0
8.1	49	41	32	28	7
13.1	54	53	39	32	15
15.1	47	41	36	30	5
20.1	34	13	5	8	0
23.1	63	48	43	35	0.7
27.1	53	47	38	23	14
10.2	60	42	43	35	13
13.2	66	57	52	48	33
17.2	74	75	53	56	61
24.2	77	75	55	64	68
1.4	75	95	76	73	98

The percentage of sites occupied in three colonies, during the period of vacation of the colonies, 1975

Date	Percentage of sites occupied		
Date	SF	WF	SCl
8.7	126	113	139
16.7	81	82	118
21.7	104	70	129
28.7	60	46	87
5.8	94	79	130
12.8	29	34	71
18.8	58	57	89
21.8	19	19	36
25.8	40	30	66
28.8	36	28	49
1.9	25	16	10
5.9	26	9	0
9.9	12	2	0
12.9	19	7	0
16.9	1	0	0
22.9	0	0	0

The number of birds present, and the number of sites occupied by pairs in the five main study areas, during the reoccupation phase, 1975

SFa		NCn		NCo		SCl		WF	
Nos	Prs	Nos	Prs	Nos	Prs	Nos	Prs	Nos	Prs
62	9	38	4	13	2	42	1	66	3
73	17	28	5	9	1	81	10	44	3
78	17	47	5	28	1	114	24	84	11
84	18	53	9	36	2	109	20	58	8
78	20	63	11	29	3	149	40	64	12
69	15	57	8	14	2	103	15	85	14
53	6	33	1	37	2	98	15	65	11
80	16	15	1	83	12	106	17	87	15
96	23	53	7	100	17	64	9	105	18
95	12	105	21	115	25	123	26	110	17
113	20	110	19	136	34	93	15	114	22
112	24	117	30	138	36	75	12	124	22
94	13	129	37	123	30	55	3	126	12
107	15	139	41	138	34	61	5	89	10
99	10	130	34	20	2	22	1	40	2
78	6	134	30	56	4	34	3	42	7
53	7	28	2	129	22	26	4	136	26
82	6	45	5	139	28	43	8	130	22
66	7	63	7	125	26			160	28
117	22	74	10	90	12			169	25
115	23	81	17	131	38			146	14
131	43	110	18	80	7			202	33
141	17	93	13	95	15			177	22
157	34	97	13	97	10			183	35
		100	11	65	9			198	29
		77	11	79	12			117	11
		114	23	87	13			149	8
		68	8	19	2			112	5
		77	7	171	33			70	4
		77	10	165	33			123	9
		61	7	162	42			98	9
		91	17	187	37			240	31
		41	6	186	44			290	72
		139	37	188	48			277	66
		159	33	174	35			353	90
		135	19	239	68			343	60
		177	47						
		191	38						
		186	51						
		157	30						
		232	62						

The number of birds present, and the number of sites occupied by pairs, in the five main study areas, during the reoccupation phase, 1976

SFa		NCn		NCo		SCl		WF	
Nos	Prs	Nos	Prs	Nos	Prs	Nos	Prs	Nos	Prs
32	3	66	12	54	8	23	2	35	1
73	16	59	6	67	15	22	2	42	4
76	13	90	20	66	12	19	1	56	3
67	12	85	21	31	3	51	5	104	19
72	10	16	3	56	7	104	18	105	20
84	13	57	11	58	8	118	25	127	22
43	4	64	10	62	7	130	35	122	18
83	10	67	10	60	8	161	41	34	4
74	12	68	12	63	6	169	41	71	10
95	27	71	13	18	4	191	58	87	8
28	4	19	2	66	9	154	38	112	15
27	1	73	10	44	6	159	41	121	21
33	2	76	15	34	6	186	51	141	24
82	12	59	9	38	3	178	41	135	24
100	24	65	12	41	4			142	28
112	26	71	10	43	8			13	2
106	21	67	12	67	9			132	27
101	12	63	7	70	10			117	16
98	18	100	25	101	21			117	21
122	31	134	36	135	43			125	25
89	17	127	29	135	37			163	41
112	24	126	24	146	40			9	1
92	13	144	35	161	44			28	2
87	8	142	39	188	66			37	4
101	14	155	43	173	54			54	5
		151	39	146	29			31	2
		156	29	147	34			31	1
		148	37	173	46			132	18
		151	35	155	35			123	13
		160	35					169	30
								179	36
								193	43
								172	29
								172	25
								213	32
								250	61
								200	26
								226	41
								189	16
								202	24
								228	25

The mean nesting density, the date of return to the colony, and the date of hatching, for 25 units of the main study areas, 1976

Colony	No. of nests	Mean Density O-5'	Mean hatching date (June)	The mean date of return (Jan 1st = 1)
NCo	29	12.6	19.1	26.2
	31	7.5	17.0	38.2
	23	11.2	17.6	32.0
	21	9.5	22.9	41.5
	52	12.0	21.9	33.6
SC1	31	4.6	22.3	44.7
	48	3.7	17.0	43.7
	28	3.6	18.7	47.0
	20	4.3	19.3	34.6
	23	2.2	19.5	47.0
SFa	26	17.1	12.1	23.9
	23	11.1	5.3	15.1
	24	15.1	8.3	17.6
	43	20.6	5.1	22.2
WF	32	13.6	14.7	24.7
	36	10.4	17.0	24.8
	42	9.3	13.3	31.0
	42	13.2	13.7	24.7
	42	12.7	16.0	32.0
	32	16.7	14.5	21.9
	41	6.6	14.6	27.0
NCn	27	5.1	19.0	32.5
	25	15.5	15.1	22.6
	30	19.3	16.5	26.6
	48	10.7	15.7	22.0

The mean nesting density, and the mean hatching dates for ten areas, 1975

Colony	Mean O-5' density	Mean hatching date (June)
SF	16.4	10.5
GC	4.3	11.3
NC1	10.3	12.0
2	11.2	12.5
3	8.3	10.5
4	4.7	13.0
5	1.3	16.0
SC2	2.2	13.0
MVB	3.4	12.8
FSC	3.1	13.8

The mean daily wind speed, the percentage of occupied sites, and the percentage of occupied sites occupied by pairs

Date	Mean daily wind speed	Percentage of occupied sites occupied by pairs (A) The number of pairs present (B) The percentage of sites occupied (C)														
		SF			WF			NCn			NCo			SCl		
		A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
14.1.75	14.5	3	1	4	0	0	3	0	0	0	0	0	0	0	0	0
17.1.75	5.7	21	67	43	21	15	27	12	5	32	13	1	14	0	0	1
23.1.75	16.7	12	25	29	5	2	14	0	0	14	0	0	7	0	0	1
27.1.75	9.1	28	121	59	24	26	41	25	21	64	17	12	43	0	0	13
31.3.75	11.4	9	22	33	6	4	25	13	7	41	18	12	41	10	3	22
25.3.75	8.5	7	30	56	5	5	40	15	10	51	11	10	53	19	12	45
9.4.75	15.5	7	23	47	10	9	33	17	6	27	12	2	10	18	4	25
11.4.75	7.5	19	129	93	15	31	78	36	37	78	24	33	84	22	52	100+
20.1.76	27.6	9	12	19	0	0	5	12	2	13	29	4	8	0	0	0
15.1.76	14.1	16	59	46	15	21	36	24	10	41	14	8	30	0	0	5
30.1.76	25.4	2	1	8	12	1	3	0	0	0	0	0	0	0	0	0
27.1.76	4.5	14	53	54	16	16	38	25	15	47	16	6	23	10	2	14
2.2.76	14.8	9	14	22	8	2	10	0	0	1	0	0	1	0	0	0
27.1.76	4.5	14	53	54	16	16	38	25	15	47	16	6	23	10	2	14
6.2.76	13.5	3	4	17	7	2	11	5	1	17	0	0	8	0	0	0
10.2.76	12.9	20	88	59	16	18	43	22	12	42	16	9	35	6	1	13

The percentage of sites occupied, and the percentage of occupied sites occupied by pairs, throughout the period of occupation of the South Face Colony, in 1975

Date	Percentage (sites)	Percentage (pairs)	Date	Percentage (sites)	Percentage (pairs)
6.1	0.6	0	5.5	116	23
7.1	17	16	13.5	109	25
9.1	16	20	20.5	123	19
10.1	35	21	27.5	126	20
14.1	4	3	3.6	113	5
16.1	28	18	10.6	108	5
17.1	43	21	18.6	114	4
20.1	46	23	22.6	126	3
23.1	29	12	30.6	113	3
27.1	59	28	8.7	126	9
30.1	60	28	16.7	81	4
3.2	66	19	21.7	104	7
10.2	67	18	28.7	60	2
17.2	70	21	4.8	94	12
24.2	74	18	12.8	29	5
3.3	73	15	18.8	58	35
11.3	72	18	21.8	19	9
18.3	56	8	25.8	40	10
25.3	56	7	28.8	36	9
31.3	33	9	1.9	25	5
4.4	59	9	5.9	26	9
9.4	47	7	9.9	12	6
11.4	93	19	12.9	19	6
22.4	99	21	16.9	0.4	0
28.4	100	24	21.9	0	0

The number of birds present, the optimum number of birds, and the expected and observed percentage of birds with light heads in the South Face and West Face colonies, during the reoccupation phase, 1976

South Face

Optimum no. of birds	Observed no. of birds	Expected percentage with light heads	Observed percentage with light heads
585	171	25	34
614	614	31	31
675	615	39	49
695	683	43	48
749	159	50	65
780	590	55	56
822	497	60	74
850	57	63	85
880	189	66	85
920	132	70	89
955	606	73	88
980	752	76	91
1015	833	79	82
1035	677	81	92
1060	753	83	95
1080	889	85	91
1086	1086	86	93
1086	862	89	90
1086	742	91	94
1086	727	93	96

West Face

129	25	19	29
136	123	24	28
149	149	33	33
154	142	35	47
166	6	43	50
174	159	47	54
184	133	52	60
190	10	56	100
198	30	60	96
207	33	65	92
214	150	69	85
221	199	72	79
230	215	76	80
237	201	79	93
244	197	82	92
252	245	85	90
256	311	86	93
260	226	88	96
267	267	90	96
276	205	92	98
282	226	97	97

The numbers of pairs responding to the greeting ceremony by kittiwaking, and the numbers not responding, at successive distances from the nest, in the North Colony New area (NCn), and the South Colony One (SCl)

Distance (feet)	NCn		SCl	
	Responding	Not responding	Responding	Not responding
1	76	42	6	4
2	170	274	26	27
3	76	305	29	41
4	49	324	26	49
5	71	463	23	66

The mean number of nests at successive distances from the nest, 1976

Distance (feet)	NCn	SCl
1	0.57	0.06
2	2.03	0.87
3	2.52	0.81
4	3.26	0.97
5	4.35	1.16

The mean clutch size, and the mean laying date, for seven units (grouped by laying date) at the Dunbar Castle Cliff colony, 1976

Mean clutch size	Mean laying date *	N
1.93	10.0	14
2.05	12.0	19
1.79	13.7	19
1.95	15.6	19
1.80	19.3	15
1.69	27.0	13
1.47	35.5	15

The number of eggs laid, the number of eggs hatched, and the mean laying date for six units (grouped by laying date) at the Dunbar Castle Cliff colony, 1976

Number of eggs	Number hatched	Mean laying date *
27	26	9.8
31	23	12.0
45	40	14.4
28	26	17.4
31	14	22.6
30	19	34.5

* 1st May = 1

Specific names of animals mentioned in the text

Adélie penguin	*Pygoscelis adeliae*
African buffalo	*Syncerus caffer*
American tricoloured redwing	*Agelaius tricolor*
Arctic tern	*Sterna paradisaea*
Black-headed gull	*Larus ridibundus*
Black-headed weaver	*Ploceus cuculatus*
Black-tail prairie dog	*Cynomys ludovicianus*
Brewer's blackbird	*Euphagus cyanocephalus*
Brown rat	*Rattus norvegicus*
Canada goose	*Branta canadensis*
Common tern	*Sterna hirundo*
Cormorant	*Phalacrocorax carbo*
Equatorial swallow-tailed gull	*Creagrus furcatus*
Fulmar	*Fulmarus glacialis*
Gannet	*Sula bassana*
Guillemot	*Uria aalge*
Herring gull	*Larus argentatus*
Kittiwake	*Rissa tridactyla*
Pacific sardine	*Sardinops caerulae*
Red-winged blackbird	*Agelaius phoeniceus*
Ring dove	*Streptopelia risoria*
Sand martin	*Riparia riparia*
Sandwich tern	*Thalasseus sandvicensis*
Vieillot's black weaver	*Melanopteryx nigerrimus*
Weasel	*Mustela nivalis*
Wildebeest	*Connochaetes taurinus*
Zebra finch	*Poephila guttata*

STATISTICS USED

Statistics used were based on the methods outlined by Snedecor and Cochrane (1971).

The majority of multivariate regression analyses were performed using a biomedical package programme (BMDO2R - revised 1972) developed at the Health Sciences Computing Facility, University of California, Los Angeles. Due to a change in the availability of the Biomedical Computer Programs final multivariate regression analyses were performed using an equivalent programme from the Statistical Package for the Social Sciences (Version 6). In addition, a Biomedical Computer Program for basic data description was used (BMDOlD - revised 1971).

The statistical method and assumptions made in these analyses are outlined in the appropriate computer manuals (Dixon 1975, Nie, Hull, Jenkins, Steinbrenner and Bent 1975).

SYMBOLS AND ABBREVIATIONS USED IN THE TEXT

b	regression coefficient in the equation $a = bx + c$
c	constant in the equation $a = bx + c$
C	constant in the equation $a = b_1x_1 + b_2x_2 + b_3x_3 \ldots + C$
df	degrees of freedom
N	sample size
N.S.	not significant
p	probability or significance level
r	correlation coefficient between two variables, written with the degrees of freedom as a subscript
R	multiple correlation coefficient
RC	regression coefficient
S.E.	standard error
S.D.	standard deviation
t	'student's' t
$\bar{x}$	mean value of x
χ^2	chi-squared